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Contribution No. 401

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BIENNIAL REPORT FOR 1945-1947 ON API RESEARCH PROJECT 43A

BACTERIOLOGICAL AND SEDIMENTATION PHASES OF THE TRANSFORMATION OF ORGANIC MATERIAL INTO PETROLEUM †

CLAUDE E. ZOBELL,* *Director*

Bacteria and allied microörganisms are responsible for the first steps in the formation of petroleum from organic matter deposited in marine sediments. This is axiomatic because, insofar as is known, the remains of all plants and animals are attacked immediately after death by bacteria or their enzymes. The extent and manner of the microbial attack of organic materials depend primarily upon environmental conditions.

In well-aerated deposits the tendency is for bacteria to oxidize organic materials largely to carbon dioxide and water. In the absence of free oxygen, anaerobic bacteria in sediments tend to deoxygenate and desulfurize organic compounds. These processes are accompanied by the liberation of carbon dioxide, hydrogen sulfide, methane, and other substances. The overall effect of anaerobes in a closed system is to convert organic materials into substances which are more petroleum-like in that the residues contain proportionately less oxygen, sulfur, nitrogen, and phosphorus than the parent material.

Although it has been demonstrated that certain bacteria produce small quantities of liquid and solid hydrocarbons as part of their cell substance, it is yet to be proved that bacteria can convert organic matter into crude oil. Most likely they contribute to the process in various ways along with geochemical, geophysical, and geological agencies. It is the purpose of this report to summarize some of the progress that has been made during the two-year period ending in December 1947 on the possible part played by bacteria in the formation or modification of petroleum or its source beds.

Methane-Oxidizing Bacteria

Methane is formed by bacteria in nearly all deposits where organic matter is undergoing anaerobic decomposition. Up to 30 per cent of the carbon in organic materials may be reduced to methane and liberated as such. Methane formation is a common feature of marine-bottom deposits rich in organic residues. Methane is almost universally found in natural gas or associated with petroleum deposits. Therefore, some attention has been devoted to the study of bacteria which oxidize or consume methane, with particular reference to the part that such bacteria may play in the petroleum problem.

Methane-oxidizing bacteria have been demonstrated in widely diverse samples of marine-bottom deposits and surface soil. They have been found in more than a hundred samples of surface sediments from estuaries, bays, the sea floor along the coast of California, and in even more soil samples. Methane-oxidizing bacteria are particularly abundant in the vicinity of oil or gas seeps, in surface soils overlayering known deposits of oil, and in swamps, mud flats, or river bottoms where there is evidence of much methane production. Such bacteria are generally absent from the lower portions of mud cores collected from the floor of the ocean.

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* Scripps Institution of Oceanography, La Jolla, Calif.

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Methane-oxidizing bacteria are believed to require free oxygen for their activity. They are occasionally detected well below the surface of sediments where conditions are strictly anaerobic. The significance of methane-oxidizing bacteria in such environments is still indeterminate. Further investigations will be required to determine whether they can catalyze the polymerization or oxidation of methane by utilizing some hydrogen acceptor other than free oxygen.

In the presence of free oxygen, methane-oxidizing bacteria utilize methane with the formation of carbon dioxide, bacterial cell substance (which is largely organic matter), and other products. Analytical results indicate that actively growing cultures may convert from 15 to 40 per cent of the carbon from methane into bacterial cell substance or other organic compounds. A study of gas ratios suggests the following empirical equation for the reaction:

$$10\ CH_4 + 16\ O_2 \rightarrow 6\ CO_2 + 4\ (HCHO) + 16\ H_2O \quad (1)$$

In this equation $(HCHO)$ represents a building block of bacterial cell substance or metabolic product, and it may be quite complex.

A small part of the organic complex synthesized by methane-oxidizing bacteria has proved to be ether soluble. From the ether-soluble fraction an unsaponifiable waxy fraction has been extracted. The yield of the latter represents less than one per cent of the carbon in the methane which was oxidized by the bacteria. Therefore, it seems doubtful if methane-oxidizing bacteria contribute significantly to the origin of oil by this mechanism. They may contribute directly or indirectly in other ways.

One of the most important indirect contributions of methane-oxidizing bacteria is to the carbon cycle. By converting methane into organic substances and carbon dioxide (which may be retained in the sediments as carbonate or readily utilized by other organisms), methane-oxidizing bacteria tend to minimize the loss of fixed carbon from the carbon cycle in sediments. The sum total of this effect may be very appreciable, considering that up to 30 per cent of the carbon in decomposing organic materials might otherwise be lost to the atmosphere as methane. Whether the activity of methane-oxidizing bacteria is an essential feature of source sediments of petroleum is problematical. The possibilities merit further consideration. Various workers have considered using methane-oxidizing bacteria in soil as indicators of subterranean deposits of gas or oil.

Methane-oxidizing bacteria catalyze the separation of hydrogen from the carbon in methane as follows:

$$CH_4 + 2\,O_2 \rightarrow CO_2 + 2\,H_2O \qquad (2)$$

This reaction probably takes place stepwise. The separation or activation of one hydrogen atom may result in the transitory formation of a methyl group ($-CH_3^+$) which might then methylate an appropriately activated organic molecule. The same line of reasoning suggests the possibility of two such nascent methyl groups combining to form ethane under certain conditions. Though highly hypothetical, the matter seems to merit some careful study.

Several different kinds of methane-oxidizing bacteria exist. The growth of some varieties is favored by the presence of organic matter. Other kinds are obligate autotrophs which grow best in a solution containing only mineral salts. All varieties of methane-oxidizing bacteria seem to require carbon dioxide and free oxygen for their multiplication. Their nitrogen requirements may be satisfied by ammonium salts or nitrate. A few methane-oxidizing bacteria can utilize amino nitrogen. Some varieties prefer fresh water or low salinity media. Other varieties thrive in sea water or higher salinity media. They flourish throughout a wide range of temperature and pH.

Although continued work on methane-oxidizing bacteria is not contemplated in the immediate future, further investigations of this group of bacteria hold promise of contributing much to our understanding of the origin of oil.

Bacterial Oxidation of Higher Hydrocarbons

Upon a basis of observations by Project 43a personnel, coupled with the published reports of other investigators, it seems reasonably safe to conclude that bacteria occur in nature which will attack virtually any kind of petroleum hydrocarbon. Unfortunately, however, very little is known regarding the intermediate and end products which result from the microbial modification of hydrocarbons. Our knowledge of the effect of environmental factors on the process is still woefully scant. Inasmuch as hydrocarbons in sedimentary materials may be destroyed or modified by microörganisms under certain environmental conditions, it follows that detailed information on these factors may provide important clues as to what constitutes a source bed of petroleum.

During the past two-year period we have been concerned primarily with a study of the action of anaerobic sulfate-reducing bacteria on hydrocarbons, the attack of complex aromatic hydrocarbons, and the rate of destruction of crude oil or narrow cuts thereof in sedimentary materials.

Long-chain paraffinic hydrocarbons have been observed to undergo rapid destruction by sulfate reducers. These bacteria attacked hexadecane with the formation of insoluble fatty acids as intermediates which underwent further degradation. One culture destroyed the equivalent of 860 mg of hexadecane per liter of sea-water medium in 30 days. The unsaturated homolog, hexadecene-1, was attacked more rapidly than was hexadecane. Out of 27 different cultures of sulfate reducers tested, 26 were found to be able to attack paraffin oil, lubricating oil, and kerosine. A like number of cultures of sulfate reducers were active in the oxidation of Pennsylvania crude oils and samples of California crude oils.

It is a point of special significance that W. D. Rosenfeld was able to demonstrate by the Thunberg technique the transfer of hydrogen from hexadecane and hexadecene-1 to methylene blue by the dehydrogenase activity of sulfate-reducing bacteria. This is believed to be the first proof of the existence of a bacterial dehydrogenase affecting hydrocarbons. Inasmuch as this enzyme can catalyze the transfer of hydrogen from hydrocarbons to methylene blue, the implication is that hydrogen may be transferred from paraffinic hydrocarbons to other hydrogen acceptors by such a mechanism. It has been suggested that such a mechanism may help to account for the conversion of paraffinic hydrocarbons into naphthenic or aromatic hydrocarbons.

The anaerobic sulfate-reducing bacteria attack aromatic and naphthenic hydrocarbons less readily than paraffinic compounds. Only a specialized few cultures were found to utilize cylic hydrocarbons having long side chains. Conclusive evidence is still lacking that sulfate reducers can split the benzene ring in the absence of any other source of energy. By adsorbing the hydrocarbons on sand it was found that a concentration equivalent to 1.0 per cent of cumene, pseudocumene, ethylbenzene, dipentene, indene, beta-methylnaphthalene, pinene, or methylcyclohexane inhibited the multiplication of sulfate reducers in nutrient media. Lower concentrations of most of these aromatic hydrocarbons were slowly attacked by sulfate reducers in media containing also a little lactate. None of the cultures was able to reproduce in media containing the aromatic hydrocarbons as the sole source of carbon and energy.

Aromatic hydrocarbons, however, are attacked by certain aerobic bacteria. Employing both growth and carbon-dioxide production as criteria of the utilization of hydrocarbons dispersed in mineral salts solution, it was demonstrated that naphthalene, anthracene, phenanthrene, 1,2-benzanthracene, and 1,2,5,6-dibenzanthracene were oxidized by bacteria in the presence of oxygen. Besides the possible importance of this observation to the petroleum problem, the publication of the results has stimulated wide interest among other bacteriologists, because some of these hydrocarbons are known to induce cancers in experimental animals. The observation suggests the possibility of developing bacteria or bacterial products which might be useful in destroying carcinogenic hydrocarbons in man or animals.

Bacterial Destruction of Crude Oil

Nearly 6,000 tests have been made to determine the bacterial oxidizability of 73 samples of crude oil from oil fields in different parts of the world. The results warrant the conclusion that virtually all types of crude oil are susceptible to bacterial attack under favorable conditions. The generalizations summarized here will be amplified in a separate paper on this subject.

There is considerable difference in the susceptibility of different oils to bacterial attack. Some crude oils, notably samples from Arabian and Venezuelan fields, were modified only slowly and slightly by bacterial cultures which, under comparable experimental conditions, rapidly destroyed or modified crude-oil samples from certain California, Pennsylvania, and Texas fields. In one series of experiments 8 different bacterial cultures caused the quantitative disappearance of 5 ml of a California crude from the surface of 50 ml of well-oxygenated mineral salts solution after twelve weeks at 28° C. Most crude oils, however, were merely modified in appearance. A good many were not perceptibly changed when a thin layer was superimposed on mineral salts solution inoculated with hydrocarbon-oxidizing bacteria.

An increase of a degree or two in API gravity was noted in some samples of crude oil under the influence of bacterial cultures for two months, as compared with corresponding sterile controls. A decrease in API gravity was observed in other crude oils subjected to the action of bacteria.

Bacteria attack crude oils more readily when the latter are dispersed in sedimentary materials than when floating on the surface of the mineral salts solution. Considerable difficulty has been experienced in obtaining data on the qualitative and quantitative changes caused by the bacteria. Neither wet nor dry extraction methods with various solvents can be relied upon to recover all of the oil from sedimentary materials. Certain volatile fractions are probably lost by some of the necessary manipulations. Gravimetric methods also have limitations for the same reason. Although these technical difficulties have not been overcome entirely, it has been demonstrated that a good many types of oils dispersed in sedimentary materials are modified or destroyed by bacteria. The rate of destruction of oil in sediments is influenced by the temperature, presence of oxygen, types of bacteria present, and other factors.

Bacteria which destroy oil in sediments under aerobic conditions have been demonstrated in 4 samples of Cuban swamp mud, 3 samples of "paraffin earth," 17 samples of garden soil, and 57 samples of surface mud from bays, estuaries, and the sea floor. Negative results have been obtained only infrequently when samples ranging in weight from 5 to 10 g have been used as inocula. These observations confirm previous reports that bacteria which are capable of attacking oil in sediments in the presence of free oxygen and a balanced mineral salts solution are quite widely distributed in nature. Under conditions favorable for their activity, such bacteria may tend to prevent the accumulation of oil in marine-bottom deposits. They may destroy oil in certain sediment samples which are exposed to free oxygen during transportation or storage.

Crude oil dispersed in sedimentary materials has been found to be attacked much more slowly and much less extensively by anaerobes than by aerobes. Bacteria which are capable of destroying oil in the absence of free oxygen have been detected in only a small percentage of the soil and sediment samples tested for their presence. Sulfate-reducing bacteria are the only anaerobes which have been shown to be able to oxidize petroleum hydrocarbons. Only a small percentage of the cultures appears to be endowed with this ability. Although sulfate reducers attack crude oil only slowly, throughout the geological ages they may have materially modified the oil in certain deposits.

Action of Anaerobes on Lipids

Because an appreciable portion of the remains of marine plants and animals is fatty material or other lipids which closely resemble hydrocarbons, considerable attention has been given to the microbial modification of such substances. Bacteria which are able to hydrolyze various glycerides and other esters of fatty acids under anaerobic conditions have been shown to occur in virtually all samples of marine-bottom deposits which have been examined. Lipolytic anaerobes have also been isolated from samples of asphalt, crude oil, oil-well brine, "paraffin earth," and tar sands. Although it has not been possible to demonstrate the hydrolysis of lipids by pure cultures of sulfate-reducing bacteria, anaerobes which are almost invariably associated with sulfate reducers in marine sediments are actively lipolytic even in the presence of hydrogen sulfide.

Lipids which have been hydrolyzed by anaerobes include pure glycerides (monopropionin, tripropionin, tributyrin, tricaproin, trilaurin, trimyristin, tripalmitin, tristearin), various other esters (amyl caproate, butyl formate, butyl stearate, phenyl stearate), and numerous oils (algal, coconut, corn, cottonseed, diatom, olive, palm, sperm). Most of these lipids, as well as fatty acids of low molecular weight, have been dehydrogenated or oxidized by anaerobic bacteria.

It is noteworthy that no fatty acid which has a molecular weight greater than caproic acid ($C_5H_{11}COOH$) has been dehydrogenated or oxidized by resting cells of lipolytic anaerobes. Some degree of correlation has been observed between the solubility and ease of dehydrogenation, although several insoluble lipids have been oxidized by anaerobic bacteria. The oxidation products have not been identified.

In the presence of a suitable hydrogen donor, such as the leuco base of methylene blue, which has been used experimentally, certain lipolytic anaerobes catalyze the hydrogenation or reduction of fatty acids. Acetic, propionic, valeric, caprylic, pelargonic, lauric, myristic, undecylenic, and lactic acids, as well as trivalerin, tricaproin, corn oil, cottonseed oil, and sperm oil have been reduced in this way in Thunberg tubes. The quantities involved were too small to permit chemical analyses of the end products of the reaction. These highly significant experiments should be repeated in a way which would provide sufficiently large quantities of the end products for careful chemical analyses, using other hydrogen donors that might occur in sediments under natural conditions.

The production of carbon dioxide and no other gas by resting cells in various fatty acid systems indicated that formic acid could function as the hydrogen donor for the hydrogenation of oleic acid ($C_{17}H_{33}COOH$), linoleic acid ($C_{17}H_{31}COOH$), and linolenic acid ($C_{17}H_{29}COOH$) under the influence of lipolytic anaerobes. An observed decrease in the iodine number of a mixture of oleic and formic acid confirmed the hydrogenation of the unsaturated fatty acid by anaerobes:

$$C_{17}H_{33}COOH + HCOOH \rightarrow C_{17}H_{35}COOH + CO_2. \quad (3)$$

A marked decrease in the iodine number of a mixture of the two acids by four different lipolytic anaerobes established the hydrogenation of linolenic acid at the expense of formic acid which was dehydrogenated:

$$C_{17}H_{29}COOH + 3\ HCOOH \rightarrow C_{17}H_{35}COOH + 3\ CO_2. \quad (4)$$

Measurements of the iodine number have also indicated the hydrogenation of corn oil and sperm oil by mixed cultures of anaerobes, the hydrogen presumably having been transferred from other organic compounds in the medium. Although the mechanism of fatty acid hydrogenation by bacteria is yet to be clarified, such reactions might help to account for the conversion of organic matter into petroleum hydrocarbons and for the general absence of olefins in crude oil.

Theoretically, the decarboxylation of fatty acids represents a simple means for the conversion of fatty acids into hydrocarbons. To date neither our own observations nor those of other investigators have yielded more than presumptive evidence for the direct elimination of the -COO group from fatty acids. The only exceptions are certain beta-keto acids, whose decarboxylation would yield methyl ketones:

$$CH_3O(CH_2)_nCH_2COOH \rightarrow CH_3O(CH_2)_nCH_3 + CO_2 \quad (5)$$

and carbon dioxide, which, with subsequent hydrogenation, yields methane. Carbon-dioxide production from acetic acid by resting cells of anaerobes in an atmosphere of nitrogen suggests a direct decarboxylation, as follows:

$$CH_3COOH \rightarrow CH_4 + CO_2 \quad (6)$$

but methane formation by this mechanism has not been confirmed.[†] Further details on lipid transformations by anaerobic microörganisms will be found in the doctorate dissertation (University of California, La Jolla, 1945), by William D. Rosenfeld, from which much of the material for this section was taken.

Anaerobic Modification of Lipids in Marine Sediments

The anaerobic decomposition of sedimentary material, originally containing about 14 per cent organic matter, in a sea-water aquarium designed to simulate

---

[†] It was demonstrated recently by H. A. Barker, University of California at Berkeley, that tagged carbon atoms (C^{14}) in the methyl group of acetic acid appeared quantitatively in methane following the action of certain bacteria. Tagged atoms in the carboxy group appeared quantitatively in carbon dioxide:

$$C^*H_3COOH \rightarrow C^*H_4 + CO_2$$
$$CH_3C^*OOH \rightarrow CH_4 + C^*O_2$$

This observation tends to substantiate the direct decarboxylation of acetic acid. Tagged or radioactive C^{14} atoms are indicated by an asterisk in these equations.

conditions in nature, was accompanied by the liberation of gases and oily material. The gas collected over a period of 85 days, exclusive of hydrogen sulfide, consisted of 21.4 per cent carbon dioxide, 74.8 per cent methane, 3.0 per cent nitrogen, and 0.8 per cent hydrogen. Although the total amount of organic matter continued to decrease throughout the duration of the experiment, there was an increase in the quantity of ether-soluble, unsaponifiable material and a decrease in the iodine number of the extract. Small subsamples of this extract were sent to W. E. Hanson, Chairman of the API chemical subcommittee, who reported the following average analysis:

Sample No.	Per Cent *C*	Per Cent *H*	Per Cent *S*	Per Cent *N*	Per Cent Ash	Deficiency
XXXVI: 160C	73.20	10.65	0.07	0.48	9.08	6.52
XXXVI: 160T	77.34	11.45	0.23	0.38	5.22	5.38

Aliquot portions of these samples were examined spectrophotometrically under the general direction of W. A. McMillan, of the committee, who reported, "The general shape of the curves (ultraviolet absorption spectra with sample in *iso*octane) indicates the presence of long chain paraffins or olefins of somewhat shorter chain length. Infrared spectra confirm the suggestion of long chain paraffins, but fail to indicate the presence of olefins. In each sample there is a hump on the side of the curve at around 255 millimicrons, which suggests the presence of an aromatic. Infrared absorption spectra were obtained in carbon tetrachloride and carbon disulfide solutions. The very strong absorptions at 3.38, 3.42, and 3.50 microns indicate positively the presence of hydrocarbons."

Regarding 2 other samples of oily or waxy, ether-soluble, unsaponifiable material produced in 143 days at 27 deg C by bacteria during the anaerobic decomposition of marine algae (XL:27-1 and XL:27-2), Dr. McMillan reported, "Except for the fact that they have higher extinction coefficients (with a Beckman ultraviolet spectrophotometer), these spectra are practically identical with those obtained last year for similar samples (XXXVI: 160C and XXXVI: 160T). The presence of aromatics could not be determined because the 250-280 millicron region, in which most bands of aromatics lie, could not be examined. There is no evidence of bands of polynuclear aromatics in the 300-330 millimicron region; however, this does not preclude their presence in small amounts." According to a report from Dr. McMillan on the interpretation of infrared spectrographs of these extracts (XL: 27-1 and XL: 21-2), aliphatic C-H linkages were indicated with some branching in the aliphatic chains. Paraffinic chains longer than eight or nine carbons were not found, and there was no indication of olefins or aromatics. Cyclopentyl naphthenes appeared to be present in appreciable quantities.

It seems significant that anaerobic bacteria have brought about an increase in the ether-soluble, unsaponifiable content, at least part of which has proved to be hydrocarbons. In other experiments, however, there has been an actual decrease in the content of unsaponifiable material, probably attributable to the presence and activity of hydrocarbon-oxidizing bacteria. Much more meticulous work will be required to explain these observations, but it may help to characterize a source bed of petroleum.

Most of the increase in unsaponifiable material in algal remains undergoing anaerobic decomposition by bacteria is believed to be due to hydrocarbons derived from bacterial cell substance, although admittedly part of it may have been released from algal cells or from mineral constituents. The synthesis of liquid and solid hydrocarbons from fatty acids as part of the bacterial cell substance has been demonstrated and previously reported.

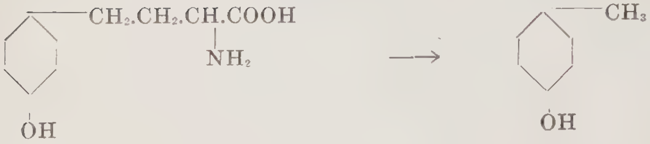
Proteins as Possible Progenitors of Petroleum

Inasmuch as from 30 to 70 per cent of the organic matter deposited on the sea floor consists of proteins, the components of which have many counterparts in petroleum, this class of compounds merits most careful consideration as possible progenitors of petroleum. The preliminary investigations of David M. Updegraff, whose doctorate dissertation (University of California, La Jolla, 1947) is on this subject, confirm the observations of other investigators that the microbial degradation of proteins results in the formation of methane, methyl mercaptan, ethyl sulfide, many fatty acids, phenol, cresol, and other products which either occur in petroleum or are closely related chemically to petroleum constituents.

Bacteria, which produce phenol and *p*cresol from tyrosine or proteinaceous compounds containing tyrosine, were found to be widely distributed in marine sediments. Ten or more such phenol-producing bacteria were demonstrated per gram (wet basis) of bottom deposits in 90 per cent of the samples from the coasts of California and Louisiana. In 64 per cent of the samples 10 or more cresol-producing bacteria were present per gram.

Eleven pure cultures of phenol-producing bacteria isolated from mud, as well as two cultures provided by Robert S. Stone of API Research Project 43b, were identified as a new species, which has been named *Pseudomonas tyrosinoclasticus.* The organism grows readily on simple nutrient media throughout a wide range of pH, E_h, osmotic pressure, and temperature. This may help to account for its rather common occurrence in different types of sediments. It is uniquely resistant to concentrations of phenol and benzoates which inhibit the growth of most bacteria.

Enrichment cultures of anaerobic bacteria from marine muds have been found to produce up to 58 per cent of the theoretically possible yield of phenol from tyrosine and up to 86 per cent of the theoretically possible yield of *p*cresol. These estimates are based upon the assumption that one molecule of phenol or cresol results from the fission of a molecule of tyrosine:



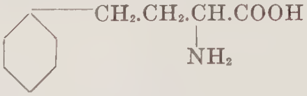
+unknown products

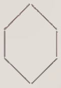
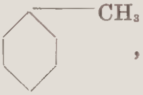
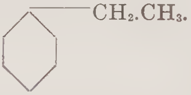
tyrosine

*p*cresol

Whether phenol or cresol is produced seems to depend partly upon the bacteria present and partly upon environmental conditions. Mixed cultures may produce both simultaneously. Anaerobic cultures produced only *p*cresol in media containing tyrosine combined by peptide linkages as in casein.

From the configuration of the molecules one might expect the simple fission of phenylalanine,



tyrosine, or allied aromatic amino acids in proteins to give rise to benzene, , toluene, , or even ethylbenzene,  However, no volatile aromatic hydrocarbon has been detected by a sensitive colorimetric method in any of more than one hundred different bacterial cultures grown in the presence of a variety of aromatic substrates. Negative results were obtained with phenylalanine, tyrosine, tryptophane, *p*hydroxybenzoic acid, benzoic acid, benzyl acetate, phenol, *p*cresol, benzaldehyde, phenylethyl alcohol, phenylethylamine, peptone, and casein. Although this does not preclude the possibility of aromatic hydrocarbons being formed, it is evident that bacteria do not catalyze the reaction under ordinary experimental conditions.

It is singularly significant that phenol, cresol, methyl mercaptan, ethyl sulfide, and other common constituents of crude oil are produced from proteinaceous materials by bacteria under conditions within the "geological fence." Further investigations will be required to determine the extent to which these or other bacterial degradation products of proteins could contribute to the origin of oil.

Microbial Oxidation of Free Hydrogen

A good many mud samples and other marine sediments have been shown to consume appreciable quantities of free hydrogen when incubated under anaerobic conditions. The activities of such bacteria may help to account for the generally observed paucity of free hydrogen in natural gases, although there is evidence that free hydrogen may be produced by the microbial fermentation or alpha-particle bombardment of organic matter.

Several species of aerobic bacteria are known to oxidize molecular hydrogen. Certain anaerobes found in sediment samples have been shown to be endowed with this ability. In the latter category are methane bacteria which activate the combination of hydrogen and carbon dioxide with the formation of methane:

$$CO_2 + 4H_2 \rightarrow CH_4 + 2H_2O. \qquad (8)$$

Most authorities agree that this is the principal mechanism by which methane is formed by bacteria. The activities of such bacteria may help to account for the depletion of free hydrogen, the formation of methane, and the disintegration of carbonates in certain deposits. They may also obtain energy from the oxidation of hydrogen for the formation of organic matter from carbon dioxide:

$$CO_2 + 2H_2 \rightarrow (HCHO) + H_2O \qquad (9)$$

The cell substance of chemosynthetic autotrophic bacteria is believed to result from the reduction of carbon dioxide to formaldehyde or similar intermediate building block which, with subsequent polymerization and additions, gives rise to more complex organic compounds.

Certain sulfate-reducing bacteria isolated from marine sediments have been shown to consume free hydrogen with the formation of hydrogen sulfide:

$$H_2SO_4 + 4H_2 \rightarrow H_2S + 4H_2O \qquad (10)$$

The multiplication of such bacteria in a mineral salts solution devoid of organic matter demonstrated that sulfate-reducing bacteria can also utilize carbon dioxide (or bicarbonate) to synthesize cell substance. The reduction of carbon dioxide was confirmed by showing that more free hydrogen was consumed than the amount required for the quantity of hydrogen sulfide formed.

Other types of anaerobic bacteria utilize free hydrogen for the reduction of amino acids, fatty acids, unsaturated organic acids, and other compounds. Cultures of *Pseudomonas tyrosinoclasticus*, which produces phenol from tyrosine, was found to consume free hydrogen, but the ultimate fate of the hydrogen was not determined.

These observations suggest that the microbial utilization of molecular hydrogen may contribute to the origin of oil and to the modification of source beds.

Occurrence of Bacteria in Older Sediments

Any one who admits the organic origin of oil cannot deny that bacteria influence the process, because normally the remains of all organisms are acted upon by bacteria, and there is no reason to believe that the organic source material of petroleum is exempt from this rule. The question confronting the microbiologist is how and to what extent do microörganisms contribute to the process. Prerequisite to the answers to this question is information on the numbers, physiological types, and evidence of activity of bacteria in source sediments of petroleum.

Large numbers of biochemically versatile bacteria have been shown to be present and presumably active in the topmost layers of marine-bottom deposits that are believed to be akin to source beds of petroleum, if not actually potential source beds. To the greatest depths sampled, living bacteria have been found in sufficient numbers to be effective in catalyzing the reactions credited to them under natural environmental conditions during the period of time that they could have been operative. For the most part, the samples upon which these conclusions are based have been collected from depths of less than 10 ft and consist of material that was deposited less than a thousand years ago, although significant numbers of living bacteria have been found in mud cores from depths exceeding 20 ft and in material believed to be more than 10,000 years old.

It is true that both total numbers and kinds of bacteria have decreased with core depth. The extrapolation of curves depicting the vertical distribution of bacteria suggests that some bacteria may be found at depths exceeding a thousand feet. Sulfate-reducing bacteria have been demonstrated in reservoir fluids from oil wells exceeding a thousand feet deep. It is questionable whether these bacteria were adventitious or indigenous species. The author found sulfate-reducing bacteria in samples of limestone-anhydrite-sulfur formation from a depth of 1,560 ft provided by the Freeport Sulphur Company and analyzed under conditions which were believed to preclude the possibilities of extraneous contamination.

On the other hand, Project 43a workers and other investigators have examined samples of pre-Pliocene coal, shale, clay, oil-bearing sands, etc., in which no living bacteria could be detected. These negative results are highly significant, particularly with cores from oil wells, because they demonstrate that it is possible to collect uncontaminated samples. It is not at all surprising that some samples do not contain living bacteria because, like other forms of life, bacteria thrive only where there are suitable sources of water, energy, and other vital requirements. There is absolutely no reason whatever to believe that bacteria will be found in all subterranean strata, notwithstanding their temperature, pressure, and salinity tolerances.

Whether bacteria occur in source sediments where organic matter is being transformed into oil or in subterranean formations where oil is undergoing modifications is the all-important question confronting us. The answer will require much careful analytical work by microbiologists and, even more important, the discriminating selection of samples for analysis from strata where there is a good probability of genetic processes ascribable to bacteria being in operation *now*. (The present tense is emphasized because, while bacteria may leave clues which we might learn to recognize, living bacteria are not likely to persist after they have done their work.) We are completely dependent upon petroleum geologists for such samples.

Through the cooperation of Morgan J. Davis of the Humble Oil and Refining Company, 13 core samples (XXIX: 170) were obtained from Timbalier Island in the Gulf of Mexico just offshore from Terrebonne Parish, Louisiana. These cores were collected with care. Sub-samples were removed for bacteriological analysis by David M. Updegraff. That the samples were not contaminated by material from the earth's surface is strongly indicated by the types of bacteria which were isolated from the cores. In most of the samples anaerobes predominated, including many which reduced sulfate and consumed hydrogen. Such bacteria were found in most samples to a depth of 177 ft. Living bacteria were not detected in 4 samples taken from depths ranging from 197 to 317 ft. The interpretation of the discontinuity of the bacterial population at 177 to 197 ft will require more information on the chemical composition of the samples from different strata. Discontinuity in the mean particle size of the sediment at 177 to 197 ft has been recorded.

Samples Received and Examined

Numerous samples of marine-bottom deposits have been collected during the last two years along the coast of California and Mexico by our own research vessel. Various cooperating agencies have provided material taken from the sea floor in other parts of the world. With three ocean-going research vessels now in operation, besides smaller craft, the Scripps Institution is prepared to collect whatever water, plankton, or surface sediment samples that may be required by API Research Project 43a. However, neither facilities nor funds are available for collecting cores of the order of a hundred or more feet in length from ocean basins.

Several hundred samples collected by our own organization as well as 223 samples of material sent to us by oil companies have been examined for the presence of specific types of bacteria which might be instrumental in the formation or modification of petroleum or its source beds. Such samples provide bacterial cultures for the experimental work, the results of which are published from time to time in this API Research volume or elsewhere. We appreciate the cooperation of contributing companies and the personal efforts of individuals in providing this material.

Conclusions

Evidence continues to accumulate from field observations and laboratory experimentation that bacteria may contribute in various ways to the transformation of organic material into petroleum. An appreciable percentage of organic material undergoing bacterial decomposition in an anaerobic environment may be converted into methane, which serves methane-oxidizing bacteria as a source of energy and carbon. Methane-oxidizing bacteria, which appear to be widely distributed in surface soil and marine-bottom deposits, probably play an important part in preventing the escape of methane into the atmosphere. Methane-oxidizing bacteria oxidize methane to carbon dioxide, organic compounds, and substances which may be closely akin to crude oil. Higher hydrocarbons are also oxidized or otherwise modified by both aerobic and anaerobic bacteria in marine sediments. Under conditions which are favorable for the activity of hydrocarbon-oxidizing bacteria, appreciable quantities of oil have been shown to be destroyed. A bacterial dehydrogenase, which activates the transfer of hydrogen from hydrocarbons to a reducible substrate, has been demonstrated.

Many additional observations have been made on the susceptibility of lipids to hydrolysis, oxidation, or hydrogenation by anaerobic bacteria. Especially noteworthy is the hydrogenation or reduction of various fatty acids by hydrogen from the leuco base of methylene blue or formic acid. The direct decarboxylation of fatty acids has not been demonstrated. During the anaerobic decomposition of organic residues in marine sediments in aquaria, a decrease in saponifiable material and an increase in unsaponifiable material has been observed. Spectrophotometric analyses indicate that at least part of the unsaponifiable material consists of long-chain paraffinic hydrocarbons. The anaerobic decomposition of proteins and amino acids has resulted in the formation of methane, fatty acids, methyl mercaptan, ethyl sulfide, phenol, and cresol, but no aromatic hydrocarbon could be detected.

It has been established that the uptake of free hydrogen by unsterilized samples of sedimentary materials in an anaerobic environment is due to the activities of bacteria, including certain sulfate reducers and methane-producers. Both types of bacteria consume carbon dioxide. Other types of anaerobic bacteria catalyze the reduction of various organic compounds in the presence of free hydrogen. Such bacteria may help to account for the generally observed paucity of free hydrogen in natural gases, and they may contribute to the transformation of organic material into petroleum.

The significance of finding living bacteria in marine sediments at different depths is briefly discussed.

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THE INFLUENCE OF HYDROSTATIC PRESSURE ON THE GROWTH AND VIABILITY OF TERRESTRIAL AND MARINE BACTERIA[1]

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Although there is abundant evidence that a rich microflora exists at the bottom of the ocean, in deep oil well brines, and in other habitats characterized by high pressure (cf. ZoBell, 1946), no clear understanding has been reached concerning the influence of pressure on the growth, viability, and metabolism of the organisms in such environments. The results of older (Certes, 1884*a*,*b*,*c*; Regnard, 1884; Certes and Cochin, 1884; Roger, 1895; Krause, 1902; Chlopin and Tammann, 1903; Hite, Giddings, and Weakley, 1914; Larson, Hartzell, and Diehl, 1918), as well as more recent, studies (cf. reviews by Macheboeuf and Basset, 1934; Cattell, 1936; Bridgman, 1946) with respect to the effects of presure on microbial processes in general are not only inadequate but in some cases apparently inconsistent. Furthermore, before the advent of the theory of absolute reaction rates in 1935 (Eyring, 1935; Glasstone, Laidler, and Eyring, 1941) no rational basis was available for the interpretation of the action of pressure on chemical reaction rates, and it has been only within the past several years that this theory has been applied to biological reactions in living cells (cf. reviews by Johnson, 1947; Johnson and Eyring, 1948.) The latter studies have shown that, in all cases, the observed effects of pressure may be profoundly modified by temperature; a fundamental relationship that had previously remained almost unnoticed.

In view of these circumstances, we have undertaken to reinvestigate the problem, with special reference to the relation between temperature and the effects of hydrostatic pressure, as well as the relation of the natural habitat of the organism to the effects observed.

The present report is in the nature of a survey of the influence of pressures up to 9,000 pounds per square inch (about 600 atmospheres), at different constant temperatures, on the growth and viability of representative species of both marine and terrestrial bacteria in pure culture, initially in the logarithmic growth phase. Extensive quantitative data are necessary for kinetic analyses of the pressure effects and will be made the subject of later investigations, as will, likewise, the significance of certain biological and other factors, such as the specific physiology of the organism, growth phase, composition of the medium, and so forth.

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METHODS

Flasks of glucose nutrient broth for aerobes and facultative anaerobes, or of brain-heart infusion containing 0.3 per cent agar for obligate anaerobes, were inoculated from cultures in the late logarithmic growth phase. For marine bacteria, the culture medium was made in natural sea water, filtered through filter paper. The flasks were incubated for 2 or 3 hours to ensure a logarithmic rate of reproduction at the start of the experiment. Sterile test tubes, size 10 by 50 mm, were then filled with aliquot portions of these cultures and were closed by sterile vaccine bottle rubber stoppers, of the type whose cap could be folded over the neck of the tube and held firmly in place by tightly wound rubber bands. Contamination was thus effectively prevented, while hydrostatic pressure was readily transmitted through the rubber stopper. The inoculated tubes were placed in a steel pressure chamber (Johnson and Lewin, 1946*a*) filled with water at the desired temperature. Pressure was then applied to the entire system by means of a connecting hydraulic pump, and the chamber immersed in a constant temperature water bath. Control cultures, corresponding in every way to those under increased pressure, were immersed in the same water bath for incubation at normal pressure. The influence of different pressures or temperatures was generally studied simultaneously by employing several pressure chambers. In all cases the experiments were repeated sufficiently to make certain of the reproducibility of the results.

RESULTS

At 30 C, a temperature generally favorable for the development of diverse terrestrial species whose "optimum" temperatures are not all the same, visible turbidity failed to develop in broth cultures of any of over 30 species incubated under a pressure of 600 atmospheres, and growth was visibly less at 400 atmospheres than at normal pressure. Moreover, cultures of most of the species were sterilized within 48 hours under 600 atmospheres at 30 C, and some by only 400 atmospheres, as shown by their failure to develop following decompression. The data for representative species of bacteria and yeasts are summarized in table 1. Yeasts appear to be more senstive, in general, than bacteria to pressure, although the opposite has been previously reported (Chlopin and Tammann, 1903).

Plate counts (table 2) showed that viability was, in some cases, much more profoundly affected than was evident from the degree of visible turbidity (table 1). Thus, after 48 hours under 300 atmospheres, cultures of *Alkaligenes viscosus* and *Proteus vulgaris*, which had grown to a marked turbidity, contained less than 100 viable cells per ml. The data show clearly that, in addition to retarding the rate of reproduction, pressure under these conditions accelerates the rate of death.

These results are evidently attributable to a direct effect of pressure during incubation, rather than to factors associated with the experimental procedure. Thus, although the accumulation of carbon dioxide during growth in the closed tubes might be expected to influence the results to some extent, more carbon dioxide was undoubtedly formed and remained in solution in cultures that developed abundantly under 300 atmospheres than in those that failed to grow at higher hydrostatic pressures. Oxygen may be ruled out as a critical factor for the aerobes, since all tubes contained the same amount of oxygen at the start.

TABLE 1

Multiplication or destruction of terrestrial microorganisms after 48 hours' incubation at 30 C at different hydrostatic pressures

(Plus signs show the degree of turbidity relative to the control culture at one atmosphere and a minus sign denotes no apparent multiplication. A "d" indicates that the culture had lost its ability to multiply following decompression.)

CULTURE	HYDROSTATIC PRESSURE IN ATMOSPHERES				
	1	300	400	500	600
Alkaligenes viscosus	++++	+++	++	−d	−d
Bacillus alvei	++++	+++	+	−	−
Bacillus brevis	++++	+++	+	−	−d
Bacillus cereus	++++	++++	−	−	−
Bacillus circulans	++++	++++	−	−	−
Bacillus megatherium	++++	++++	+	−	−d
Bacillus mesentericus	++++	++++	+++	++	−d
Bacillus mycoides	++++	++++	+	−	−d
Bacillus subtilis	++++	++	+	−	−
Clostridium chauvei	++++	++++	++	−	−
Clostridium histolyticum	++++	++++	+++	−	−d
Clostridium putreficum	++++	++++	++	−	−
Clostridium septicum	++++	++	+	−	−
Clostridium sporogenes	++++	+++	++	−	−
Clostridium welchii	++++	++++	+	−	−
Escherichia coli	++++	++++	+++	++	−
Micrococcus lysodeikticus	++++	++	−	−d	−d
Mycobacterium phlei	++++	+++	++	−d	−d
Mycobacterium smegmatis	++++	++	+	−	−d
Proteus vulgaris	++++	++	−	−	−d
Pseudomonas fluorescens	++++	++++	+++	−	−
Sarcina lutea	++++	+++	+	−	−d
Serratia marcescens	++++	−	−	−	−
Staphylococcus albus	++++	+++	+++	−	−
Staphylococcus aureus	++++	++	−	−d	−d
Streptococcus lactis	++++	++++	++++	++	−
Hansenula anomala	++++	++	−d	−d	−d
Saccharomyces cerevisiae	++++	++++	−d	−d	−d
Saccharomyces ellipsoideus	++++	+	−d	−d	−d
Schizosaccharomyces octosporus	++++	−	−d	−d	−d
Sporobolomyces salmonicolor	++++	+	−d	−d	−d
Torula cremoris	++++	++++	++	−d	−d

With regard to anaerobes, no significant amount of oxygen diffused through the rubber stopper closure to retard growth, as was shown by the absence of appreciable recolorization of methylene blue solutions that had been partially reduced at the start by hydrosulfite, then incubated under conditions similar to those of the cultures. The suddenness with which cultures were compressed or decompressed, during short exposures to high pressures, was shown by plate counts to have no appreciable effect on viability.

In general, tables 1 and 2 would indicate that the various species are more sensitive to pressure than would be expected according to previous reports to the effect that, under some conditions, terrestrial bacteria can withstand pressures of 10 to 50 times those that we find retard multiplication or actually kill (Chlopin and Tammann, 1903; Hite, Giddings, and Weakley, 1914; Larson, Hartzell, and Diehl, 1918; Basset and Macheboeuf, 1932). A number of causes may be responsible for such apparent discrepancies. In any event, the influence of temperature as a factor in the net effect of pressure is of special significance.

TABLE 2

Plate count of nutrient broth shortly after inoculation and after 48 hours' incubation at 30 C at various hydrostatic pressures

CULTURE	INITIAL COUNT PER ML	PLATE COUNT PER ML AFTER 48 HOURS AT				
		1 atm	300 atm	400 atm	500 atm	600 atm
Alkaligenes viscosus	700	160,000,000	<100	<100	<10	0
Bacillus cereus	1,600	40,000,000	650,000	700	<100	0
Bacillus circulans	20,000	11,000,000	880,000	265,000	200	20
Bacillus mesentericus	1,900	21,000,000	230,000	60,000	10	0
Bacillus mycoides	2,250	2,000,000	160,000	114,000	700	0
Bacillus subtilis	1,600	14,000,000	600,000	42,000	30	8
Proteus vulgaris	2,600	142,000,000	<100	<100	<10	0
Pseudomonas fluorescens	10,000	95,000,000	21,000,000	5,000,000	810	80
Sarcina lutea	4,700	36,000,000	67,000	22,000	400	12
Serratia marcescens	300	64,000,000	<100	<100	<10	0
Staphylococcus albus	4,400	77,000,000	80,000,000	57,000	700	350
Staphylococcus aureus	800	156,000,000	174,000,000	9,000	0	0
Streptococcus lactis	4,000	273,000,000	149,000,000	70,000,000	160,000	18,000

In studying the relation of the pressure effect to temperature, experiments with a majority of the species listed in table 1 were repeated at 20 C, 30 C, and 40 C, for periods of 4, 2, and 1 days' incubation, respectively. All cultures developed well at normal pressure, but the influence of increased pressure was strongly dependent upon the temperature of incubation, as shown by the results summarized in table 3. Most of the species failed to develop visible turbidity under 300 atmospheres at 20 C, yet the same organisms grew abundantly under the same pressure at 40 C. Furthermore, although none of the cultures developed visibly at either 20 C or 30 C under 600 atmospheres, at least four species (*Bacillus mesentericus*, *Bacillus subtilis*, *Escherichia coli*, and *Streptococcus lactis*) grew fairly well under this pressure at 40 C. Thus, within the range of temperatures that permit cultures to develop at normal pressure, the growth-retarding effects of increased pressure are diminished at the higher temperatures. The same relation has been reported in connection with the rate of growth of *E. coli* in synthetic medium during short periods of the early logarithmic phase (Johnson and Lewin, 1946*b*).

Marine bacteria indicate the same general relation between temperature and the effects of pressure, with a somewhat greater resistance to pressure on the whole (table 4). In addition, there is a correlation between the sources from which these species were isolated and their ability to grow under pressure. Thus, the luminous bacteria (*Achromobacter fischeri*, *Achromobacter harveyi*, and *Photobacterium splendidum*), as well as other species (*Achromobacter thalassius*, *Bacillus cirroflagellosus*, *Micrococcus infimus*, *Pseudomonas pleomorpha* and *Vibrio hyphalus*) obtained at or near the surface of the ocean, tend to resemble the terrestial organisms in their response to pressure. On the other hand, some species, *Bacillus submarinus* and *Bacillus thalassokoites*, in particular, isolated from depths where the pressure approximates 500 atmospheres, grew prolifically under 600 atmospheres at 30 C as well as at 40 C and were obviously more resistant to the effects of 400 and 500 atmospheres than the terrestrial bacteria. Mixed microflora, from mud freshly collected from the sea floor at depths up to 12,000 feet, multiplied abundantly at all pressures and temperatures that were studied. Growth in some cases was more rapid under 400 to 600 atmospheres than at normal pressure. To these facts we can add the observation that certain sulfate-reducing bacteria, isolated from oil well brines several thousand feet below the earth's surface, are metabolically more active when compressed at 400 to 600 atmospheres than at 1 atmosphere. The ability to grow and carry on metabolism as well or better under increased pressure would seem to justify coining the word *barophilic* to characterize such organisms.

TABLE 3

Relative turbidity of cultures in nutrient medium after four days' incubation at 20 C, two days at 30, or one day at 40 C at different hydrostatic pressures

All cultures listed below showed four-plus (++++) growth in the controls incubated at normal pressure

CULTURE	300 ATMOSPHERES			400 ATMOSPHERES			500 ATMOSPHERES			600 ATMOSPHERES		
	20 C	30 C	40 C	20 C	30 C	40 C	20 C	30 C	40 C	20 C	30 C	40 C
Alkaligenes viscosus	++	+++	++++	++	++	++	−	−	−	−	−	−
Bacillus brevis	−	+++	++	−	+	+	−	−	−	−	−	−
Bacillus megatherium	−	++++	+++	−	+	++	−	−	−	−	−	−
Bacillus mesentericus	−	++++	++++	−	+++	++++	−	++	++++	−	−	++++
Bacillus subtilis	−	+++	++++	−	++	++++	−	−	+++	−	−	++
Clostridium bifermentans	++	++++	++++	−	−	+++	−	−	−	−	−	−
Clostridium chauvei	−	++++	++++	−	++	+++	−	−	−	−	−	−
Clostridium histolyticum	−	++++	++++	−	−	+++	−	−	−	−	−	−
Clostridium putreficum	−	++++	++++	−	++	++	−	−	−	−	−	−
Clostridium septicum	−	+	++	−	−	+	−	−	−	−	−	−
Clostridium sporogenes	−	++++	++++	−	++	+++	−	−	−	−	−	−
Clostridium welchii	−	++++	++++	−	+	++	−	−	−	−	−	−
Escherichia coli	++	++++	++++	−	+++	++++	−	++	++++	−	−	++++
Mycobacterium phlei	−	+++	++++	−	++	+	−	−	−	−	−	−
Mycobacterium smegmatis	−	++	++	−	+	+	−	−	−	−	−	−
Pseudomonas fiuorescens	++	+++	++++	−	++	++++	−	−	+++	−	−	−
Sarcina lutea	++	++	++++	−	+	++	−	−	−	−	−	−
Staphylococcus albus	++	++	++++	−	+	++	−	−	−	−	−	−
Staphyiococcus aureus	−	+++	++++	−	++	+++	−	−	−	−	−	−
Streptococcus lactis	+++	++++	++++	+	++++	++++	−	++	++++	−	−	++++

TABLE 4

Relative turbidity caused by the multiplication of marine bacteria in nutrient broth for six days at 20 C, four days at 30 C, or one day at 40 C at different hydrostatic pressures

(All cultures listed below, except those marked with an asterisk, which failed to grow at 40 C, showed four plus (++++) growth in the controls incubated at normal pressure

CULTURE	300 ATMOSPHERES			400 ATMOSPHERES			500 ATMOSPHERES			600 ATMOSPHERES		
	20 C	30 C	40 C	20 C	30 C	40 C	20 C	30 C	40 C	20 C	30 C	40 C
Achromobacter fischeri	++++	++	*	++	−		−	−		−	−	
Achromobacter harveyi	++++	++++		+	++++	−	−	−	−	−	−	−
Achromobacter thalassius	−	++++	++	−	−	+++	−	−	−	−	−	−
Bacillus abysseus	+	++++	++++	−	++++	++++	−	+	++++	−	−	++++
Bacillus borborokoites	++	++++	++++	−	++++	++++	−	++	++++	−	−	++++
Bacillus cirroflagellosus	++	+++	*	−	++		−	−		−	−	
Bacillus submarinus	++	++++	++++	+	++++	++++	−	++++	++++	−	++++	++++
Bacillus thalassokoites	+++	++++	++++	++	++++	++++	−	++++	++++	−	++++	++++
Flavobacterium okeanokoites	++++	++++	++++	++++	++++	++++	++	++++	++++	−	−	++++
Flavobacterium uliginosum	++++	++++	++++	++++	++++	++++	−	++++	+	−	−	−
Micrococcus infimus	+	++++	*	−	+		−	−		−	−	
Photobacterium splendidum	++++	++++	*	++	+++		−	+		−	−	
Pseudomonas pleomorpha	++	++++	*	++	+++		−	++		−	−	
Pseudomonas vadosa	++	++++	++++	++	++++	++++	−	++++	++++	−	−	++++
Pseudomonas xanthochrus	++++	++++	*	++++	+++	+	++	++	++	+	+	−
Vibrio hyphalus	−	−	*	−	−	−	−	−		−	−	
Mixed microflora from mud	++++	++++	++++	++++	++++	++++	++++	++++	++++	++++	++++	++++

All the pure cultures listed in table 4 had been maintained at atmospheric pressure for several years, most of the time at around 4 C, prior to the experiments described, yet the barophilic properties of the deep-sea organisms were not lost. This provides evidence of a genetic character, in adaptation to the high pressure of the habitat, as one might expect from general considerations. At the same time, however, it must be emphasized that the total effects of pressure are likely in all cases to depend upon the temperature, and a complete picture is obtainable only after exhaustive studies of the reciprocal relationships of both factors. Data concerning *Pseudomonas xanthochrus* (table 4) provide a striking illustration. At 40 C no growth was apparent at normal pressure, but cultures grew at 400 and 500 atmospheres. Under these conditions, *Pseudomonas xanthochrus* might be regarded as an obligate barophile. At 20 C, however, although it grew under as much as 600 atmospheres, growth was more abundant under lower pressures, including atmospheric. Lower temperatures remain to be studied, and it is difficult to predict whether evidence of barophilism will then be found, but it is reasonable to expect that the sensitivity of this, as well as other species, to pressure will be more pronounced as the temperature is decreased. Likewise, it remains to be seen whether there exist in nature any bacterial species that normally require high pressures for growth.

DISCUSSION

Although the results of this study confirm those of previous investigations in showing that, under given conditions, various species of terrestrial bacteria exhibit a considerable range in sensitivity to the effects of pressure, they indicate that broth cultures in the logarithmic phase are generally nore susceptible to the growth-retarding and disinfecting action of pressure than was formerly appreciated. The influence of temperature as a factor modifying the effects of pressure has been shown by present data to be of considerable importance, and may account in part for apparent discrepancies between these and previously reported results. Moreover, on the basis of the more recent studies of the pressure-temperature relationships of microbial enzyme activity (Johnson, Brown, and Marsland 1942; Brown, Johnson, and Marsland, 1942; Johnson, Eyring, and Williams, 1942; Johnson, Eyring, Steblay, Chaplin, Huber, and Gherardi, 1945; Johnson, Kauzmann, and Gensler, 1948), denaturation of proteins (Johnson and Campbell, 1946; Johnson, Baylor, and Fraser, 1948), and related phenomena some specific mechanisms, among the numerous and incompletely known complex of reactions concerned in growth and viability, may be postulated as controlling factors in the influence of pressure. Briefly, they are as follows:

First, it is evident that the action of pressure, under the conditions of the present experiments, is directly on chemical reactions: rate processes and equilibria. No significant change in concentrations of reactants resulted from the application of pressure, per se, to the purely liquid systems, i.e., systems without any considerable gas phase. The effects of pressure that are observed through changes in sol-gel systems, oxidation-reduction potentials, solubility, dissociation, enzyme reactions, etc., at given concentrations of reactants depend upon the molecular volume change accompanying the limiting reaction. Where large molecules are concerned, as in biological systems, the volume change is frequently large, of the order of 50 to 100 cm^3 per mol, and the influence of pressures amounting to only 500 or 600 atmospheres is therefore pronounced.

In growing cells over considerable periods of time, both the internal and extracellular chemical environments undergo many changes, and it is not possible in the present stage of knowledge to single out any one or two limiting reactions whose modification by pressure would account for the total result. It is possible, however, to point to certain fundamental actions of pressure, particularly on enzyme systems and protoplasmic gels, that parallel the results obtained with growth and viability. Thus, it has been shown that oxidative enzyme reactions, such as luminescence, proceed with a large volume increase of activation. At temperatures below the normal optimum, a pressure of 500 atmospheres greatly retards the reaction by opposing the molecular volume increase. At higher temperatures, and most noticeably above the optimum, the critical enzyme undergoes a reversible denaturation that proceeds with an even larger volume increase of reaction. At these temperatures, the net effect of pressure is to increase the rate of the reaction by reversing the denaturation of the enzyme to a greater extent than opposing the catalytic reaction. At intermediate temperatures, the net effect is also intermediate, for pressure acts on two simultaneous reactions with opposite results on the observed phenomena. In luminescence, the effects of pressure are in the same direction as cooling, and the same trend is apparent in the present data on growth. Thus, pressure is more effective at the low temperatures, as further cooling would be at normal pressure. Also, at temperatures too high for growth (*Pseudomonas xanthochrus*) at normal pressure, the application of pressure permits growth to take place. Pressure has also been shown to retard the irreversible thermal denaturation of proteins, and this, too, might be expected to contribute an aid to viability under pressure at relatively high temperatures.

The disinfecting action of pressure is less readily explained. Cells might be expected to lose their viability, however, when their energy-yielding reactions are sufficiently retarded, and by opposing such reactions, pressure might be expected to accelerate death. Irreversible changes under pressure have also been noted in protoplasmic gels (Marsland, 1942), another possible factor involved in the killing action of pressure.

In undertaking to account for species differences in susceptibility to pressure, two important relationships must be taken into account.

In the first place, the reciprocal relationship between temperature and the effects of pressure is conditioned by the specific temperature characteristics of the system of organism concerned. For psychrophilic organisms, the beneficial effects of pressure might be expected to occur at lower temperatures than with mesophilic species, and the retarding effects at much lower temperatures, even though the volume changes were the same in the reactions affected. For thermophilic organisms, on the other hand, it is reasonable to expect that pressure will act strongly against growth and viability at ordinary temperatures, but at very high temperatures, above their normally high optimum, pressure will enable growth to occur as well as help to preserve viability. Thus, deep oil well brines at high temperatures are not unlikely to yield "obligate barophiles."

In the second place, there is a possibility that the organisms living in deep-sea muds and other habitats under high pressures have become genetically so adapted to their environments that metabolic reactions occur through mechanisms involving no appreciable volume increase, or even involving a significant volume decrease of activation. In this event, pressure would either have little effect or actually favor their activities. Although experimental methods and the theoretical basis are available, the whole field remains very largely to be explored. Practical as well as fundamentally significant consequences can be expected to result from future investigations on the action of hydrostatic pressure.

The authors are pleased to acknowledge their indebtedness to Jean S. ZoBell for her assistance in carrying out the experiments.

SUMMARY

Representative species of mesophilic terrestrial bacteria and yeasts of the genera *Alkaligenes*, *Bacillus*, *Clostridium*, *Escherichia*, *Micrococcus*, *Mycobacterium*, *Proteus*, *Pseudomonas*, *Sarcina*, *Serratia*, *Staphylococcus*, *Streptococcus*, *Hansenula*, *Saccharomyces*, *Schizosaccharomyces*, *Sporobolomyces*, and *Torula* were studied in regard to the action of hydrostatic pressure on the development of pure cultures, initially in the logarithmic growth phase in broth. Species of the genera *Achromobacter*, *Bacillus*, *Flavobacterium*, *Micrococcus*, *Photobacterium*, *Pseudomonas*, and *Vibrio*, isolated from the sea at various depths, were similarly studied. In both cases, the influence of temperature (by incubating at 20, 30, and 40 C) on the effects of pressure was investigated.

At 30 C, the terrestrial organisms developed abundantly within 48 hours at normal pressure, but none multiplied perceptibly under 600 atmospheres, and failure to grow after decompression showed that some had been sterilized by this pressure during the period of incubation. Growth of most terrestrial organisms was visibly retarded by a hydrostatic pressure of 400 atmospheres and plate counts indicated that growth was slower and death faster at only 300 atmospheres than at normal pressure.

The marine species, particularly *Bacillus submarinus* and *Bacillus thalassokoites*, which were isolated from depths where the pressure approximates 500 atmospheres, grew readily under 600 atmospheres at both 30 and 40 C in the laboratory. Mixed microflora from muds of the same depths apparently grew faster under pressure. The term "barophilic" is introduced to characterize species whose growth or metabolism is favored by pressure. Other species from near the surface of the sea were intermediate, or more nearly resembled terrestrial bacteria in their sensitivity to pressure. In one case (*Pseudomonas xanthrochrus*) cultures developed under 400 to 600 atmospheres at 40 C, a temperature too high for growth of the culture at normal pressure. The same pressures retarded growth at lower temperatures.

The influence of pressure on pure cultures in all cases depended upon the temperature. In general, lower temperatures markedly accentuated the growth-retarding and disinfecting effects of pressure. Conversely, at higher temperatures, the net effect of pressure was less pronounced, or in some cases acted in the direction of opposing the unfavorable effects on growth and viability caused by the high temperature.

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DIFFUSION IN BIKINI LAGOON

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(Contribution from the Scripps Institution of Oceanography, New Series, No. 403)

Abstract--During the preliminary survey at Bikini, the state of turbulence in the lagoon was determined from three types of measurements: simultaneous measurements of surface current and wind speed, measurements of diurnal temperature fluctuations at various depths, and measurements of the rate of mixing of the oxygen-rich reef water with the body of the lagoon water. These measurements lead to reasonably consistent values for the coefficient of vertical diffusion. The coefficient of horizontal diffusion was estimated on the basis of past observations and of measurements of the lateral spread of dye markers. Its estimated value compares favorably to a value computed from the lateral spread of radioactive material deposited during the underwater atom-bomb burst.

Introduction--Two factors were principally responsible for reducing the intensity of radioactivity of the lagoon water after each bomb burst: radioactive decay and diffusion. Diffusion studies were undertaken in the spring of 1946 to aid in a prediction of how soon after each burst the lagoon might be safe to enter.

By analogy with the process of diffusion due to random molecular motion it is customary to define a coefficient of eddy diffusion A by the equation [SVERDRUP, JOHNSON, and FLEMING, 1946, pp. 69, 92-93].

$$M = -A\,\partial S/\partial n \quad \ldots\ldots (1)$$

where M is the amount of substance which per unit time diffuses through a unit surface area, and $\partial S/\partial n$ the concentration gradient along a line normal to that surface. The coefficient A is usually more than a million times the corresponding molecular coefficient. Its value depends not only on wind speed, current shear, density gradient, and the scale of the phenomenon, but also on the diffusion direction. According to previous measurements, the coefficient of vertical eddy diffusion. A_v varies from one to 320 cm^2/sec; that of horizontal eddy diffusion A_h from 2×10^6 to 4×10^8 cm^2/sec [SVERDRUP, JOHNSON, and FLEMING, 1946, pp. 483-486].

Too little is known about diffusion to make an estimate of the numerical values of the coefficient pertaining to Bikini Lagoon. Preliminary work at Bikini was therefore directed toward determining these values. Once they were known the rate of spread and dilution of any initial contamination could be computed.

The original plan provided for an experiment, for which radioactive materials were to be flown from the United States and dropped into the lagoon. This experiment was cancelled, but fortunately existing natural conditions provided several excellent methods for estimating the values of the diffusion coefficients.

Part I--Preliminary survey, March to April 1946

Surface current and wind speed--For winds exceeding 6.5 m/sec (13 knots) the stress applied by the wind on a unit surface area equals [SVERDRUP, JOHNSON, and FLEMING, 1946, p. 490]

$$2.6 \times 10^{-3} \rho\, U^2 \quad \ldots\ldots (2)$$

where ρ is the density of air, U the wind speed at about ten m above the water. Assume the wind stress to be balanced by the shearing stress in the water of magnitude

$$A'_v\, \partial u/\partial z_x \quad \ldots\ldots (3)$$

where u is the horizontal current at a depth z (z = 0 at surface, z = h at bottom), and A'_v is the coefficient of vertical eddy viscosity, assumed constant from top to bottom. As a very rough approximation let

$$u = u_0\,(1 - 2z/h) \quad \ldots\ldots (4)$$

so that the net volume transport $\int_0^h u\,dz$ between surface and bottom equals zero. The vertical current gradient, and hence the shearing stress, is then independent of depth. Combining (2), (3), and (4) and setting $\rho = 1.25 \times 10^{-3}$ g/m^3, h = 5000 cm (165 ft), gives

$$A'_v = 2.6 \times 10^{-3}\,\rho\,U^2h/2u_0 = 8.15 \times 10^{-3}\,U^2/u_0 \quad \ldots\ldots (5)$$

In Figure 1 u_0 has been plotted against U for various values of A'_v. Comparison with observations, also entered in Figure 1, indicates a value for A'_v between 200 and 300 cm^2/sec.

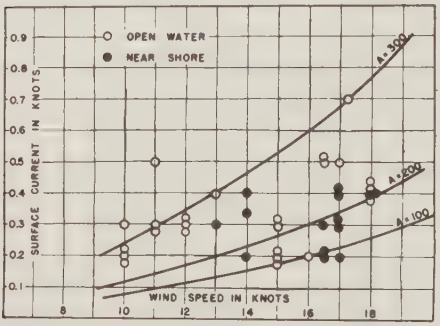

Fig. 1--Circles represent simultaneous observations of wind speed and surface current; lines give the theoretical relationships according to (5) for various values of the eddy viscosity coefficient

The waters in Bikini Lagoon are so thoroughly mixed that the temperature difference between surface and bottom rarely exceeds 0.5°F [FORD, 1949]. Consequently one may expect the numerical value of the diffusion coefficient for radioactive material approximately to equal the eddy viscosity coefficient [SVERDRUP, JOHNSON, and FLEMING, 1946, p. 477].

Diurnal temperature fluctuations--Solar radiation induces a slight diurnal variation in temperature within a very thin surface layer where practically all heat is absorbed. Let the temperature deviation from the mean surface temperature be given by the equation

$$(\Delta\phi)_0 = \theta \cos (2\pi/T)t \quad \ldots\ldots (6)$$

where θ is the amplitude of the temperature cycle at the surface, and T is the period of the cycle, here 24 hr. As a result of vertical mixing subsurface layers partake in the diurnal cycle according to the equation [SVERDRUP, JOHNSON, and FLEMING, 1946, pp. 135-136]

$$(\Delta\phi)_z = \theta e^{-rz} \cos\,[(2\pi/T)\,t - rz] \quad \ldots\ldots (7)$$

where $(\Delta\phi)_z$ is the temperature deviation at the depth z from the mean temperature at that depth. and r is related to the coefficient of vertical eddy conductivity A''_v by the equation

$$A''_v = \pi/T\,r^2 \quad \ldots\ldots (8)$$

The effect of horizontal diffusion, and of horizontal and vertical advection, is neglected in (7).

The amplitude of oscillation decreases exponentially with depth, and the phase lag relative to the surface cycle increases linearly with depth. The parameter r, and hence the eddy conductivity A''_v, can be computed from either the measured amplitudes of oscillation, or the measured phase lag. The numerical value for the eddy diffusivity should be approximately that of the eddy conductivity.

Temperatures were measured at the surface and at three depths by means of reversing thermometers and bathythermographs. These measurements were made once every two hours for more than 24 hours at two anchor stations. Coefficients of A''_v were computed from the amplitude ratios, and the measured phase lags used as a check.

For the eastern station, located about three miles southwest of Bikini Island, these measurements gave values of A''_v between 260 and 320 cm^2/sec (see Fig. 2). For the western station, about seven mi from the western reef, this method gave values of A''_v of about 2000 cm^2/sec (see Fig. 3). This unreasonably large value was ascribed to vertical advection due to sinking of water in the western third of the lagoon, a feature which would tend to increase the amplitude of subsurface temperature fluctuations. Calculations gave a sinking speed of about two mi/hr, a value consistent with other considerations. The fact that A''_v at the eastern station was not unreasonably small would indicate that the rising of water due to upwelling is confined to a narrow zone adjacent to the reef.

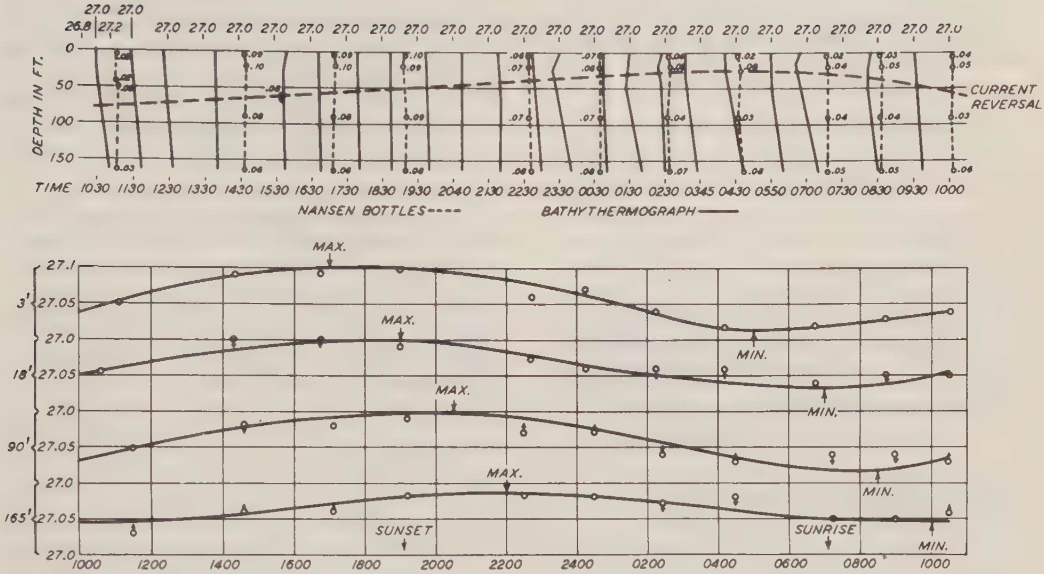

Fig. 2--Diurnal variations in temperature at various depths in the eastern portion of Bikini Lagoon; upper portion of figure gives vertical sections of temperature from measurements by means of bathythermographs and Nansen bottles; from these the variations in temperature at four fixed depths were computed and plotted in the lower portion of the figure

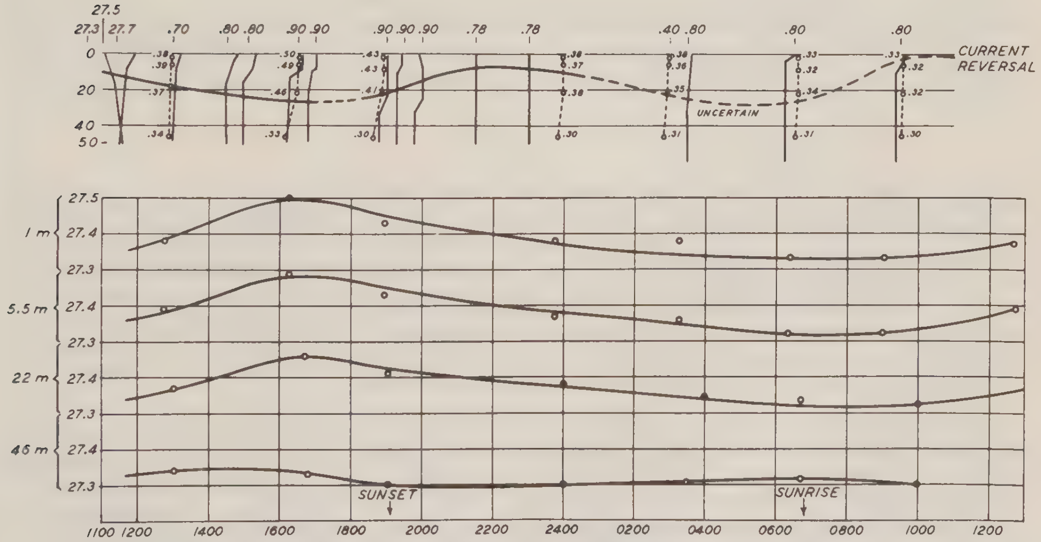

Fig. 3--Diurnal variations in temperature at various depths in the western portion of Bikini Lagoon

Diffusion of reef water--Trade-wind waves drive water over the northern and eastern reef, thereby causing a continuous current from the ocean into the lagoon [MUNK and SARGENT, 1948]. At noon, especially during low tide, the water is appreciably warmed as it flows over the wide reef; it also increases in salinity, and it becomes saturated with oxygen. Upon flowing into the lagoon this reef water can be recognized as a distinct water type. The rate of mixing of the reef water with the main body of the lagoon water provides a means of estimating the coefficient of diffusion.

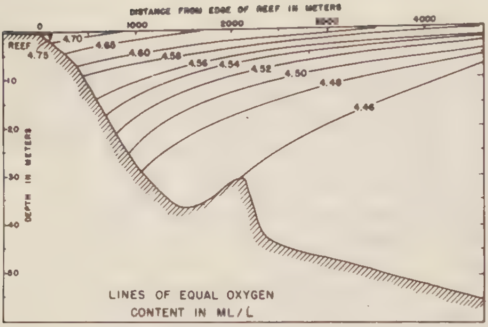

Fig. 4--Oxygen-rich reef water enters lagoon over shallow reef shown in the upper left corner; lines of equal oxygen content indicate rate of mixing of reef water with main body of water in Bikini Lagoon; direction of vertical section, S 40° W

Figure 4 shows lines of equal oxygen content in ml/L along a vertical section normal to the reef between Bikini and Amen Islands. Oxygen concentration was used rather than salinity or temperature, because the percentage difference between the oxygen content of the reef water and that of the lagoon water was larger than the corresponding differences for temperature and salinity.

The organic production or consumption of oxygen amounts to less than 0.01 ml/L per day [SARGENT and AUSTIN, in press], and can be neglected without introducing an appreciable error. Any change in concentration s in a fixed unit volume is assumed to result from vertical diffusion and horizontal advection [SVERDRUP, JOHNSON, and FLEMING, 1946, pp. 153-163].

$$\partial s/\partial t = A_v\, \partial^2 s/\partial z^2 - u\, \partial s/\partial x \quad \ldots (9)$$

where u is the speed of water flow, directed away from the reef along the positive x-axis. Assuming steady station conditions, $\partial s/\partial t = 0$, and

$$A_v = (u\, \partial s/\partial x)/(\partial^2 s/\partial z^2) \quad \ldots\ldots\ldots\ldots (10)$$

The mean value for u was determined from measurements with the Von Arx current meter [VON ARX, 1948] and amounted to 20 cm/sec (0.4 knots). Values of $\partial s/\partial x$ and $\partial^2 s/\partial z^2$ were determined graphically from Figure 4. The coefficient of vertical diffusion was then computed according to (10) for various positions in the vertical section. Values of A_v increase with distance from the surface and decrease with distance from the reef. The average value for A_v is 260 cm^2/sec.

Summary of measurements of vertical diffusion--Disregarding the measurements of diurnal temperature fluctuations in the western lagoon, the various methods give the following numerical values of A_v: 200-300, 260, 320, 260 cm^2/sec. According to Ekman [SVERDRUP, JOHNSON, and FLEMING, 1946, p. 494] the eddy viscosity A'_v in homogeneous water varies with the wind speed U according to the equation

$$A'_v = 4.3 \times 10^{-4}\, U^2 \quad \ldots\ldots\ldots\ldots (11)$$

provided U exceeds 6.5 m/sec. Taking a wind speed of 7.5 m/sec (14.5 knots) as representative of conditions during March and April, (11) gives $A'_v = 240\ cm^2/sec$, in excellent agreement with results from measurements at Bikini. It must be emphasized, however, that the methods used are all subject to large observational errors, and furthermore that personal judgment enters to a large degree in the interpretation of these measurements. In order to predict diffusion of radioactive material from the bomb bursts an average value of 250 cm^2/sec was assumed, with 200 and 300 cm^2/sec representing the lower, and upper limits, respectively. Unfortunately the bomb bursts were delayed, and took place during wind conditions very much different from the ones assumed here; the results were therefore applicable only to a limited extent.

Horizontal diffusion--According to SUTTON [1932], and to unpublished studies by SVERDRUP [1946] the coefficient of horizontal diffusion A_h depends principally upon the scale of the phenomenon. Let r be a representative radius of the area under consideration. Experiments with dye markers ($r = 10^3$ cm) dropped from planes gave values for A_h of about $5 \times 10^2\ cm^2/sec$. For large-scale oceanographic phenomenon r is of the order of 1000 km (10^8 cm) and A_h on the average $5 \times 10^7\ cm^2/sec$. For these two extreme examples the value of r varies by a factor of 1:100,000, whereas the ratio A_h/r varies only from 0.2 to 0.5. As a representative value for Bikini the ratio A_h/r = 0.4 was chosen.

Part II--Diffusion of radioactive materials deposited by the atomic bomb

Observations--The following discussion refers only to the underwater burst [Baker]. The concentration of radioactivity is given in arbitrary radiation units (aru), which have been corrected for radioactive decay on the basis of laboratory experiments with sea water. The analysis is restricted to the first three days after the burst (from B + 1 to B + 3), because following this period a shift in wind direction greatly complicated the picture. Changes in the distribution of radioactivity should be due only to processes of diffusion and advection, except for the possibility of re-activation of water passing over radioactive wreckage, or over contaminated portions of the lagoon bottom.

Table 1--Number of measurements of radioactivity

Depth	Time			Total
	B + 1	B + 2	B + 3	
ft				
0	41	42	42	125
10	24	29	36	89
75	15	30	35	80
150	12	21	31	64
Total	92	122	144	358

Table 1 shows the number of measurements at various depths in a region of about six-mi radius surrounding the target area.

Water samples were collected by the Oceanographic Division of the Radiological Safety Section of Joint Task Force One in addition to their other duties. The samples were analyzed by K. G. Scott of that Section and the radioactivity determined to at least three significant figures. These measurements are more closely spaced and much more accurate than any equivalent set of measurements taken in the past; they constitute the best material that has been available for the study of diffusion in the sea.

As is so often the case when quality and quantity of measurements are improved, the phenomenon under consideration reveals itself to be more complex than has been previously assumed. The spottiness of the distribution is striking; on B + 2, for example, a concentration of 60 aru was measured within 1500 ft of three observations of about two aru. Since many, if not most, small regions of high radioactivity must have escaped observations, the analysis must be confined to the main features.

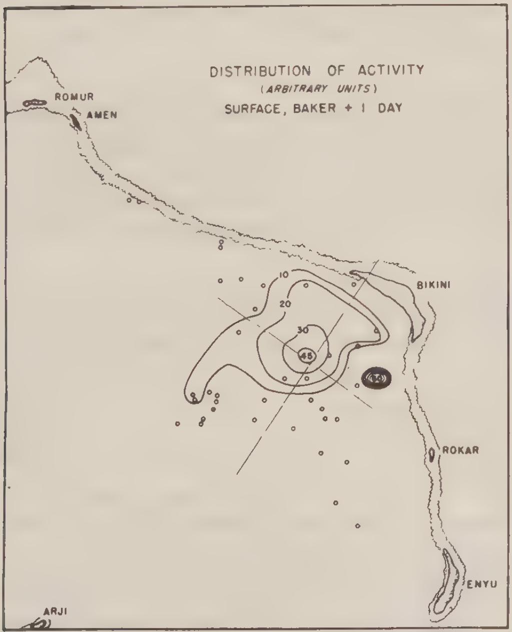

Fig. 5--Distribution of radioactivity in surface waters of Bikini Lagoon; Baker + 1 day

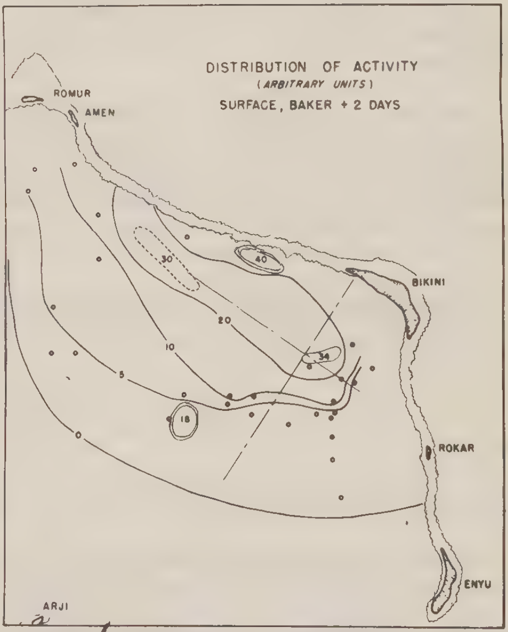

Fig. 6--Distribution of radioactivity in surface waters of Bikini Lagoon; Baker + 2 days

Qualitative description of the diffusion of contaminated water--In examining the distribution shown in Figures 5 to 7, one should hold in mind that they are based on measurements extending over many hours, rather than on simultaneous measurements.

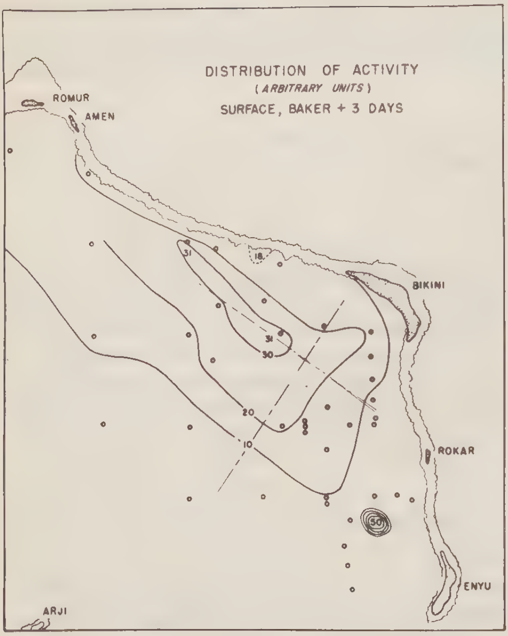

Fig. 7--Distribution of radioactivity in surface waters of Bikini Lagoon; Baker + 3 days

The surface distribution on B + 1 (see Fig. 5) shows one well-defined maximum southwest of Bikini Island; another maximum south of Bikini Island. By the second day (see Fig. 6) the concentration is elongated along a northwest-southeast axis, and the center of concentration has moved several miles to the northwest. The contamination has spread at right angles to the direction of drift. A number of secondary high-concentration areas are present which were not apparent from the surface distribution on the first day. Among these, the area with a maximum of 41 aru probably resulted from upwelling against the reef. The surface distribution on the third day (see Fig. 7) has drifted further towards the northwest.

The most prominent feature the of the changes in surface distribution of radioactivity is therefore a lateral spread of the contamination, superimposed upon a slow drift. The direction of drift is toward the northwest, in the direction the wind was blowing. The drift speed is about 0.1 knots.

The highest concentrations are usually found at depths of about 75 ft, sometimes even deeper. Unfortunately measurements at subsurface depths are more scarce, and not even the main features of the distribution are well established. The flow is directed opposite to that at the surface, and its speed is of the order of 0.03 knots.

The general pattern of movement, or advection, is shown in Figure 8. Regions of high concentration for various times and at various depths are entered, and the probable direction of drift indicated. The presentation is speculative. Measurements at the surface and ten ft are fairly consistent, and will therefore be grouped together in our computations. Near the surface the radioactivity appears to be most concentrated about four km southwest from Bikini Island, along an axis pointing in the direction of flow and labeled advection axis. At greater depth the radioactivity is centered about ten km southwest of Bikini.

Computation of the coefficient of horizontal eddy diffusivity--At the time t = 0, assume the total amount of radioactive material to be concentrated along the line x = 0. Then at any time t and distance x the concentration S is given by the normal distribution equation [McEWEN. 1946].

$$S = S_0 e^{-(x/\sigma)^2/2}/\sigma\sqrt{2\pi} \quad \ldots\ldots\ldots\ldots\ldots\ldots (12)$$

where

$$\sigma = \sqrt{2A_h t} \quad \ldots\ldots\ldots\ldots\ldots\ldots (13)$$

is the standard deviation, S_0 the total radioactivity per unit length of line, and A_h the kinematic coefficient of eddy diffusivity in the x-direction. The coefficient A_h is assumed constant.

Equation (12) has been fitted to the observed distribution of radioactivity at the surface and at ten ft depth, for B + 1, B + 2, and B + 3 (see Fig. 9). Each point represents the mean distance x of a radioactivity contour from the advection axis. The positive x-axis extends in a southwesterly direction, that is, away from the reef. Diffusion toward the northeast is inhibited by the reef; therefore observations along the positive x-axis have been given more weight in fitting the curves than observations along the negative x-axis.

According to Figure 9, the measured concentration near the center always exceeds the concentration maximum given by (12), indicating perhaps that the assumption of constant A_h may not be valid.

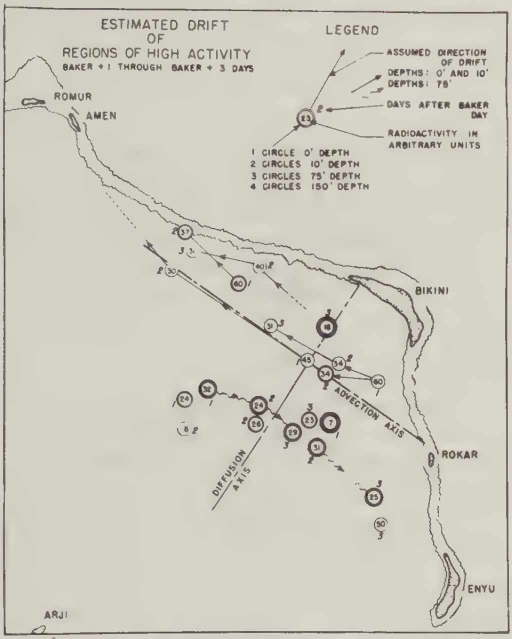
ESTIMATED DRIFT
OF
REGIONS OF HIGH ACTIVITY
BAKER + 1 THROUGH BAKER + 3 DAYS
LEGEND
ASSUMED DIRECTION OF DRIFT
DEPTHS: 0' AND 10'
DEPTHS: 75'
DAYS AFTER BAKER DAY
RADIOACTIVITY IN ARBITRARY UNITS
1 CIRCLE 0' DEPTH
2 CIRCLES 10' DEPTH
3 CIRCLES 75' DEPTH
4 CIRCLES 150' DEPTH
ROMUR
AMEN
BIKINI
ROKAR
ENYU
ARJI
ADVECTION AXIS
DIFFUSION AXIS

Fig. 8--Location of regions of high radioactivity during B + 1 through B + 3, and their estimated drift

The total amount of radioactive material in the surface layers is proportional to S_0, the area under the curve through the points. Numerical values of S_0 are listed in the second column of Table 2. For the first two days S_0 remains approximately constant. For the third day it is one-fourth larger, probably due to upwelling of material from greater depth. All observations for the third day were consequently multiplied by a factor of 0.80 to make the distribution during the three days comparable. The third column in Table 2 lists the standard deviations of the curves in Figure 9.

Let σ_1, and σ_2 designate values of the standard deviation at t_1 and t_2, respectively; according to (13)

$$A_h = (\sigma_2^2 - \sigma_1^2)/2\ (t_2 - t_1)\ \ldots\ldots\ (14)$$

where A_h represents the mean value of the coefficient between times t_1 and t_2.

Values of A_h in Table 3 have been computed according to (14) from the observed changes in distribution between various times, where it has been assumed that the distribution on B + 1 can be fitted by a normal curve. It is of some interest to compute the time interval which would have to elapse for an initial distribution along a line x = 0 to assume the distribution found at B + 1. According to (13) this time interval must equal

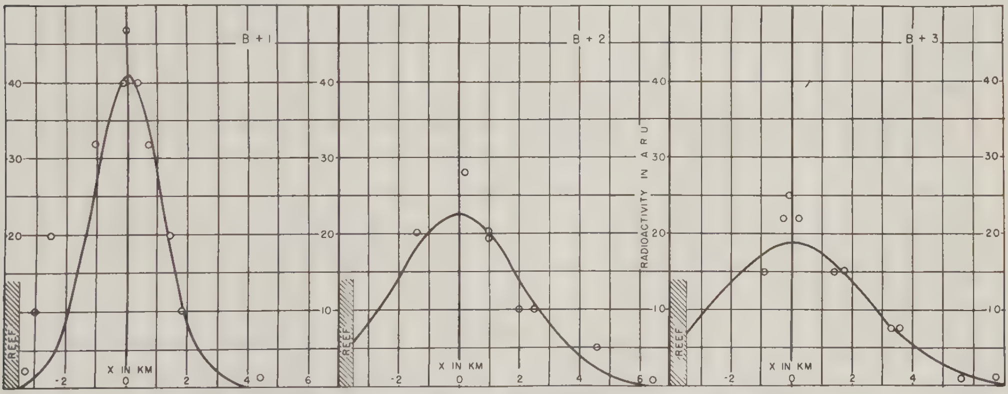

Fig. 9--Observed and computed distribution in radioactivity

Table 2--Quantity of radioactive material in the surface layers, and standard deviation of its distribution about advection axis

Time	S_0	σ
days	aru	cm
B + 1	1.29×10^7	1.15×10^5
B + 2	1.23×10^7	2.10×10^5
B + 3	1.57×10^7	2.52×10^5

Table 3--Values of the coefficient of horizontal eddy diffusivity

t_1	t_2	A_h
day	day	cm²/sec
B + 1	B + 2	1.8×10^5
B + 2	B + 3	1.2×10^5
B + 1	B + 3	1.5×10^5

$$t = \sigma^2/2A_h$$

Setting $\sigma = 1.15 \times 10^5$ cm, and $A_h = 1.5 \times 10^5$ cm^2/sec, gives t = 1/2 day. This value is of the correct order of magnitude.

Evaluation of A_h at subsurface depths was carried out for only one case, a contaminated area at a depth of 150 ft (see Table 4), which diffused noticeably between B + 1 and B + 2. For these two days the concentrations near the center were 7.0 and 6.5 aru, respectively. The mean radius of the one aru contour equals two standard deviations, because the normal curve has a value of 1/7 of the maximum ordinate at a distance of two standard deviations from the center. Measuring the mean radius of the one aru contour, the standard deviation can be computed, and A_h evaluated according to (14).

Table 4--Computation of A_h at 150 ft depth

Time	Mean radius of 1 aru contour	σ	A_h
day	cm	cm	cm^2/sec
B + 1	1.64×10^5	0.82×10^5	0.5×10^5
B + 2	2.50×10^5	1.25×10^5	

The coefficient of diffusion at 150 ft is about 1/3 the value of the coefficient at the surface. It may be significant that the drift at that depth has about 1/3 the speed of the surface drift.

Summary of Part II--A representative value for the radius of the contaminated area between B + 1 and B + 3 is 3 km or 3×10^5 cm. The mean value for A_h at the surface was found to be 1.5×10^5 cm^2/sec. This gives $A_h/r = 0.5$ cm/sec, in excellent agreement with a ratio of 0.4 proposed prior to the burst.

A determination of the coefficient of vertical diffusivity from the radioactivity data does not appear feasible, due to difficulties of separating the vertical diffusion from vertical advection (upwelling against the reef), and due to the extreme patchiness in the distribution of radioactive material. This patchiness, although it prevents more refined methods of analysis, is in itself a finding of considerable interest. It indicates not only patchiness in the initial distribution of radioactivity as it was deposited by the atomic bomb, but also that the turbulent eddies which spread the contamination over a larger area did not appreciably reduce the patchiness during the first three days.

Acknowledgment--This work represents results of research carried out for the Hydrographic Office, the Office of Naval Research, and the Bureau of Ships of the United States Navy Department under contract with the University of California.

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INVESTIGATIONS

THE ACCELERATION OF SPORE DISINFECTION BY URETHAN AND ITS RETARDATION BY HYDROSTATIC PRESSURE[1]

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Kinetic evidence has shown that urethan catalyzes a reversible or irreversible denaturation[4] of certain enzymes and proteins, viz., the light-emitting system of luminous bacteria (Johnson, Eyring, Steblay, Chaplin, Huber, and Gherardi, 1945), crude yeast invertase (Johnson, Kauzmann, and Gensler, 1948), T-5 bacteriophage (Foster and Johnson, unpublished), and purified tobacco mosaic virus (Fraser, Johnson, and Baker, unpublished), through reactions that may be reversed or retarded by hydrostatic pressures of 600 atmospheres and less. The influence of pressure on the equilibrium or on the rate of these reactions shows that they proceed with a large molecular volume increase of reaction or of activation, respectively. Moreover, since the reactions are readily observed, as a rule, only at increased temperatures, they evidently involve also large heats of reaction or of activation, the actual increase in temperature required depending upon the specific system concerned and certain other factors such as pH. In at least one case, contrasting with the above, urethan denatures a protein, methemoglobin (Schlegel and Johnson, 1949), at room temperature through reactions that exhibit no net effect of pressure.

The present study was undertaken to determine how urethan would influence the disinfection of bacterial spores at both normal and increased hydrostatic pressure. The methods employed have been adequately described in a previous report (Johnson and ZoBell, 1949) and need not be enlarged upon except to state that, in making plate counts, the specimens containing urethan were diluted to such an extent that the concentration of the drug introduced into the medium was always too low, as shown by control experiments, to influence the number of colonies that developed. The same strain of *Bacillus subtilis* was used in this as in the previous study.

RESULTS

At 25 C, corresponding portions of a suspension of *B. subtilis* spores in phosphate-buffered NaCl solution, containing 69 to 77 × 10^3 viable spores per ml at the start, and urethan concentrations ranging from 0.01 to 2.0 M evidenced no appreciable change in viability over a period of 60 minutes. In repeated experiments the counts all agreed within 10 per cent of the control. At 93.6 C, however, concentrations of 0.1 M urethan or higher caused a perceptibly greater decrease in viability within the same period of time, and this effect was opposed by a hydrostatic pressure of 600 atmospheres (table 1).

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[1] Aided by grants from the American Cancer Society through the Committee on Growth, and from the American Petroleum Institute Research Project 43A.

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[3] The authors are pleased to acknowledge their indebtedness to Jean S. ZoBell for her assistance in conducting the experiments.

[4] Though widely used, the expression "protein denaturation" is variously defined. In all cases, however, the reactions leading to denaturation result in the loss of a characteristic property of the native protein and involve large entropy changes and, generally, high heats of reaction or activation. It is in this sense that we employ the term.

TABLE 1

Influence of hydrostatic pressure on the viability of Bacillus subtilis spores in phosphate-buffered NaCl solution containing different concentrations of urethan

CONCENTRATION OF URETHAN	CONTROL AT 25 C AND 1 ATM	93.6 C FOR 30 MINUTES		93.6 C FOR 60 MINUTES	
		1 atm	600 atm	1 atm	600 atm
None	69,000	21,000	59,000	100	20,000
0.01 M	71,000	21,000	48,000	70	19,000
0.03 M	70,000	20,000	44,000	140	19,000
0.10 M	68,000	21,000	41,000	20	13,000
0.33 M	70,000	15,000	36,000	0	12,000
1.00 M	68,000	4,100	26,000	0	7,400

TABLE 2

Plate counts of Bacillus subtilis spores in phosphate-buffered NaCl solution with and without urethan, after being heated at 93.6 C for different periods of time and at different hydrostatic pressures

EXPT.	URETHAN	TIME	1 ATM	100 ATM	200 ATM	400 ATM	600 ATM
A	None	0 (initial)	73,000				
	None	30 minutes	28,000	33,000	37,000	46,000	53,000
	None	60 minutes	500	800	7,300	17,000	21,000
	None	90 minutes	<10	30	120	1,700	3,900
	1.0 M	0 (initial)	76,000				
	1.0 M	30 minutes	5,800	8,700	17,500	32,000	49,000
	1.0 M	60 minutes	<10	<10	70	2,100	5,300
	1.0 M	90 minutes	<10	<10	<10	<10	150
B	None	0 (initial)	64,000				
	None	30 minutes	31,000	39,000	45,000	53,000	
	None	60 minutes	770	940	6,100	8,000	
	None	90 minutes	10	40	110	1,400	
	1.0 M	0 (initial)	63,000				
	1.0 M	30 minutes	4,800	9,000	15,000	33,000	
	1.0 M	60 minutes	<10	<10	<180	3,200	
	1.0 M	90 minutes	<10	<10	<10	30	

With a given concentration that caused a pronounced effect, e.g., 1.0 M urethan, the "protective" action of pressure increased with rise in pressure from 100 to 600 atmospheres. The data from two typical experiments are recorded in table 2.

The rate of decrease in number of viable spores at 93.6 C, under both normal and 600 atmospheres pressure, and with 0.0, 0.5, and 2.0 M urethan, respectively, is indicated in figure 1. In all cases there is an initial lag, or period of relatively slow disinfection, that lasts much longer than the approximately 70 seconds required for temperature equilibration when the specimens are introduced into the constant temperature glycol bath at 93.6 ± 0.03 C. The rate of disinfection increases progressively with time. For this reason, together with the fact that the theoretical relationship between the number of individual spores dying per unit of time and the rates of the chemical reactions that bring about death remains obscure, any quantitative estimate of the net volume change involved in such reactions would have no clear meaning. On the other hand, from the fact that a pressure of only 600 atmospheres causes such a pronounced retardation in the disinfection process, it is apparent that some limiting reaction or reactions take place with a large volume increase, quite possibly of the order of 100 ml per mol, as in the protein denaturations referred to above, which can be analyzed with some assurance. Furthermore, it is apparent that urethan, in effect, lowers the temperature for disinfection, as it does in catalyzing the denaturation of

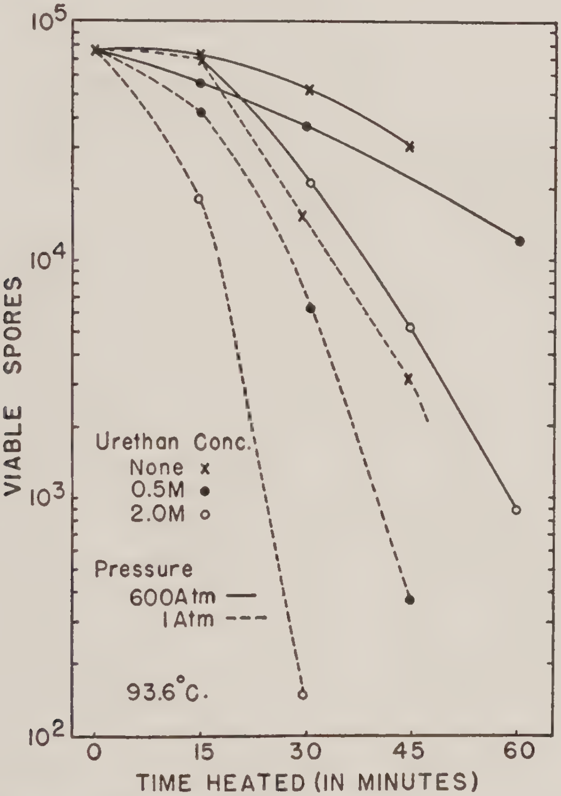

Figure 1. Influence of urethan and hydrostatic pressure on the rate of disinfection of *Bacillus subtilis* spores in phosphate-buffered NaCl solution at 93.6 C.

proteins. Finally, pressure retards the process, with as well as without urethan, again resembling the phenomena observed with this drug in connection with better-defined systems at increased temperatures.

The data presented herewith serve to emphasize the fundamental relationship between temperature and the effects of hydrostatic pressure. In addition to specific metabolic and other reactions studied earlier, the viability of spores may be favorably influenced by moderately increased hydrostatic pressures, which help to counteract the destructive effects not only of high temperatures but of some chemical agents that promote such effects. Thus, in natural environments characterized by both high temperatures and high pressures, e.g., some of the deep oil well brines, it is reasonable to expect an indigenous flora of barophilic thermophiles (ZoBell and Johnson, 1949), whose existence and activities are to a significant extent made possible through the effects of pressure.

SUMMARY

At 25 C, concentrations of urethan up to 2 M have no effect on the viability of *Bacillus subtilis* spores in phosphate-buffered NaCl solution, over short periods of observation. Disinfection of these spores at 93.6 C, however, is appreciably accelerated by 0.1 M urethan, and greatly accelerated by concentrations of 0.5 to 2.0 M. The rate of disinfection with as well as without urethan is retarded by hydrostatic pressure, the amount of the retardation increasing with pressure from 100 to 600 atmospheres.

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THE RETARDATION OF THERMAL DISINFECTION OF BACILLUS SUBTILIS SPORES BY HYDROSTATIC PRESSURE[1]

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Hydrostatic pressures of 5,000 atmospheres or more at ordinary temperatures of 20 to 30 C are known to kill bacteria and their spores, as well as to inactivate viruses and to denature proteins and enzymes (cf. reviews by Macheboeuf and Basset, 1934; Cattell, 1936; Bridgman, 1946). On the other hand, pressures of a lower order of magnitude, around 500 atmospheres, have been shown to have an opposite effect, viz., they retard the killing of bacteria at temperatures above their optimum for growth (Johnson and Lewin, 1946*a*,*b*) and reverse or retard the thermal inactivation of enzymes as well as the denaturation of proteins (Johnson, 1947; Johnson and Eyring, 1948; Eyring, Johnson, and Gensler, 1946; Johnson, Baylor, and Fraser, 1948; Johnson, Kauzmann, and Gensler, 1948). The present study concerns the previously unreported influence of these lesser pressures on the disinfection of spores by heat.

METHODS

Nutrient glucose, 0.5 per cent NaCl agar slants were inoculated with a single strain of *Bacillus subtilis* (from the United States Bureau of Standards) and incubated at 37 C for 3 to 4 weeks. The spores were suspended in a 0.5 per cent NaCl solution and buffered at pH 7.0 by 0.75 per cent K_2HPO_4 plus 0.25 per cent KH_2PO_4. They were centrifuged, washed three times, and finally emulsified in sterile solution of the same composition, resulting in a suspension of individual spores, practically devoid of vegetative cells, which maintained uniform viability of about 8×10^7 per ml for several weeks when stored in the refrigerator.

Specimens for exposure to heat were made by diluting the stock suspension 1:1,000, giving about 80,000 spores per ml. In some experiments this dilution was made with distilled water instead of buffered salt solution, with the result that the medium, though not actually salt-free, contained only 1 part of potassium phosphate per 100,000 of solution and 1 part of NaCl per 200,000 of solution. The diluted stock suspension was introduced aseptically into a series of small sterile glass tubes, as illustrated in figure 1*B*. The tubes were closed with

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[3] The authors are pleased to acknowledge the assistance of Jean S. ZoBell with the experiments.

sterile rubber stoppers and placed in water-filled brass "bombs" (figure 1*C*), which could be connected with a source of pressure from a hydraulic pump (figure 1*D*) or to a dummy connection (figure 1*E*). By means of a manifold with 8 outlet lines, pressure from the pump was simultaneously applied to 8 bombs. These bombs, along with 8 at normal pressure, were then introduced into a glycol bath maintained at the desired temperature, ±0.03 C. Calibration of the rate of heating showed that temperature equilibration at 92.5 C was obtained within 70 seconds. Cooling was somewhat faster, when at specified intervals a pair of bombs, at increased and normal pressure, respectively, were removed and placed in cold water.

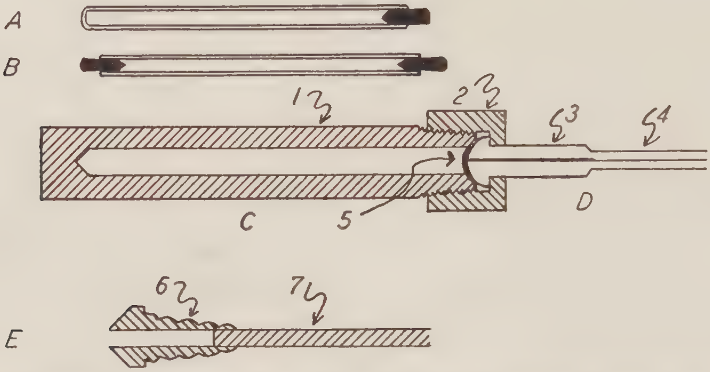

Figure 1. Diagram of apparatus used for disinfection of spores at normal and increased hydrostatic pressure.

A and *B*, two types of small glass tubes, $\frac{3}{16}$ inches in outer diameter by $2\frac{5}{8}$ inches long, capacity about 0.5 ml, for exposing specimens to heat in a brass "bomb" (*C*), $\frac{9}{16}$ inches in outer diameter and $\frac{1}{4}$ inch inner diameter. The bomb itself (*1*) was first filled with water, the tube introduced, and then connected by hex nut (*2*) to outlet (*3*) of the oil line (*4*) from a hydraulic pump. A small circle of sheet rubber (*5*) prevented the mixing of oil from the pump with the water surrounding the specimen tube in the bomb. Similar bombs (*1*) were used for specimens heated at normal pressure, but instead of the connection *D* (parts *3* and *4*), a "dummy" connection (*E*) was attached. The base (*6*) of this connection had an air space, allowing the water in the bomb to expand when heated without generating a high pressure. The solid connecting rod (*7*) made a convenient handle. With assembly (*C*) pressure was applied before heating and released after cooling. Heating was accomplished by placing both types of bombs in a constant temperature glycol bath for the desired interval of time.

Dilutions for plate counts were made in the buffered NaCl solution referred to above. After plating in the usual manner, in glucose nutrient agar containing 0.5 per cent NaCl at 45 C, the agar was allowed to harden, and a second layer, about 2 mm deep, of the same medium was added to prevent spreading of the colonies. This procedure resulted in very consistent, and generally higher, counts from a given specimen.

RESULTS

During short periods of compression there was no appreciable change in number of viable spores in the completely liquid medium whether pressure was applied at once or in steps, or was released gradually or suddenly (table 1). These results would be anticipated on the basis of general considerations. Over long periods of time at 25 C there is a slow loss of viability, amounting to about a 75 per cent decrease in 48 hours at normal pressure. When compressed to 600 atmospheres, however, this decrease is accelerated, especially toward the latter

TABLE 1

Influence of short periods of compression and influence of rapidity of decompression on viability of spores of B. subtilis subjected to 600 atmospheres (hydrostatic) at 25 C

PRESSURE	PERIOD OF COMPRESSION	PLATE COUNT WHEN DECOMPRESSED	
		Slowly	Rapidly
1 atm (control)	0 (initial)	(53,500)	(53,500)
200 atmospheres	1 minute	55,000	53,000
600 atmospheres	1 minute	49,000	53,000
600 atmospheres	30 minutes	53,000	57,000
600 atmospheres	3 hours	50,000	45,000
600 atmospheres	3 minutes 3 times	51,000	53,000
600 atmospheres	3 minutes 10 times	52,000	49,000

About 30 seconds were required to apply pressure, which could then be released rapidly (in less than 1 second) or slowly (over a period of about 60 seconds). The plate counts agree within the limits of experimental error.

TABLE 2

Data from two typical experiments on the disinfection of B. subtilis spores at 25 C and 93.6 C, and at 1 and 600 atmospheres of hydrostatic pressure

EXPT.	PERIOD OF TIME	CONTROL AT 25 C AND ONE ATM	CONTROL AT 25 C AND 600 ATM	HEATED TO 93.6 C AT ONE ATM	HEATED TO 93.6 C AT 600 ATM
A	0 (initial)	81,000			
	7 minutes	80,000	76,000	53,700	73,000
	15 minutes	83,000	70,100	1,600	59,000
	30 minutes	81,000	64,500	20	11,200
	45 minutes	79,000	61,000	<10	280
	60 minutes	82,000	52,500	<10	55
	4 hours	74,000	17,500	<10	<10
	24 hours	32,500	560	0	0
	48 hours	19,500	62	0	0
B	0 (initial)	69,000			
	15 minutes	68,000	64,000	7,000	39,000
	30 minutes	70,000	70,000	600	9,000
	45 minutes	67,000	40,000	10	700
	60 minutes	71,000	31,000	0	48
	90 minutes	73,000	20,000	0	<10

Stock spore suspensions in buffered NaCl solution were diluted 1:1,000 with distilled water for these experiments.

part of the experiment, with the result that less than 10 per cent of the spores remain viable after 48 hours (table 2*A*). This acceleration very likely takes place through the same mechanism that leads to disinfection of spores under much higher pressures within shorter periods of time (as in the experiments of Larson, Hartzell, and Diehl, 1918; and others).

At 93.6 C, the rate of loss of viability is, as expected, enormously faster, but the influence of pressure is in the opposite direction to that at 25 C, viz., pressure retards the rate of killing. At both temperatures the influence of pressure on the rate of killing is analogous to its influence on protein denaturation, accelerating at low temperatures but retarding at high. The fact that the effect is in opposite directions at the different temperatures, however, shows that the mechanism of the limiting reaction is not the same in the two cases.

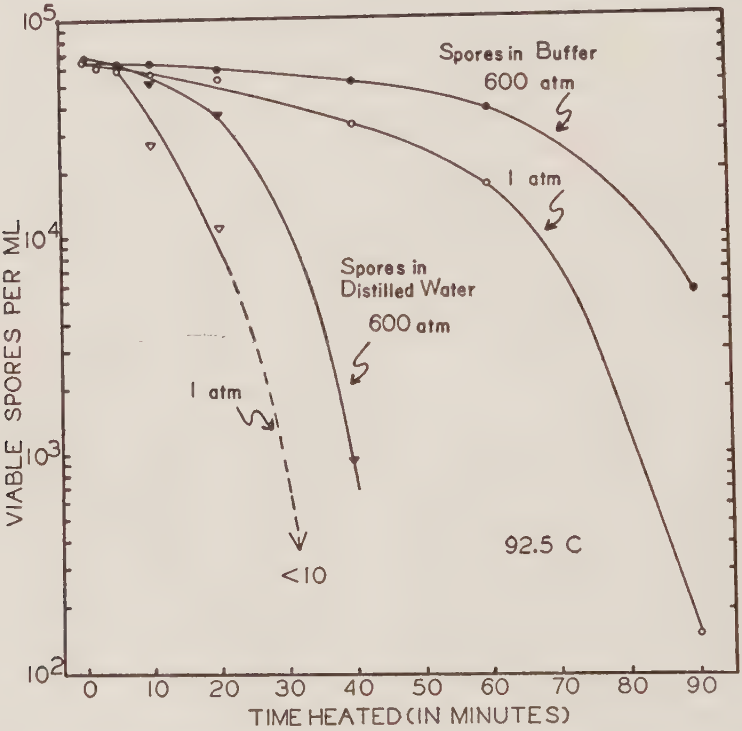

Figure 2. Rate of disinfection of *B. subtilis* spores in 0.5 per cent NaCl buffered at pH 7.0 by 1.0 per cent phosphate, and in a 1:1,000 distilled water dilution of this solution (labeled "Distilled Water") at 92.5 C, and at hydrostatic pressures of 1 and 600 atmospheres, respectively. Points on the curves for buffered NaCl solutions are the average of three repeated experiments; others are from one experiment.

The action of hydrostatic pressure in denaturing proteins and killing bacteria and spores, possibly through a similar mechanism, has not been clearly elucidated, but it has been suggested that it involves a drastic crushing of the solvent, with concomitant loss in stability of the highly ordered, native protein molecule

(Eyring, in paper by Johnson, Baylor, and Fraser, 1948). The opposal of denaturation by pressure at high temperatures, however, clearly depends on the volume change of activation (Glasstone, Laidler, and Eyring, 1941; Stearn and Eyring, 1941) in the limiting reaction. In the protein denaturations studied thus far, the volume change is generally positive and large, amounting to an increase of 50 to 100 ml per mol in going from the normal to the activated state, as shown by the quantitative relation between the amount of pressure and its influence on the observed rate. Since protein denaturation is most likely an important factor in disinfection by heat, it is rather to be expected that a moderate hydrostatic pressure of 600 atmospheres should retard the rate of thermal disinfection.

The kinetics of bacterial disinfection, under the influence of heat and of chemical agents, has been the subject of extensive investigation and discussion (cf., e.g., Rahn, 1943, 1945). In some cases the rate of decrease in the number of viable cells conforms to the kinetics of a first order reaction, as if the alteration of a single critical molecule (gene?) per cell were sufficient to kill that cell. In our experiments, however, the rate of disinfection either in buffered salt solution or distilled water bore no resemblance to a first order chemical reaction. The average plate counts of three repeated experiments with the same stock suspension of spores is illustrated in figure 2, which shows that the number of viable spores decreases slowly at first, then quite rapidly. The initial "lag" is much longer than the time required for temperature equilibration, and was repeatedly observed. In distilled water the rate is faster than in buffered salt solution, but the general shape of the curve is the same. The retarding effects of pressure on disinfection are most apparent during the initial, slow rate and seemingly less during the subsequent fast rate. These facts are susceptible of a number of reasonable interpretations, but until conclusive evidence is available it would scarcely be profitable to list or discuss them. The point of particular interest is that although pressure accelerates the killing of spores at ordinary temperatures, it retards their killing at high temperatures, both cases paralleling the influence of pressure on protein denaturation.

SUMMARY

Spores of *Bacillus subtilis*, suspended in buffered salt solution, pH 7.0, slowly lose their viability at 25 C, and this decrease in viability is accelerated by a hydrostatic pressure of 600 atmospheres. During short periods of compression, the rapidity of decompression or repeated subjection to pressure has no appreciable influence on viability.

At 92.5 C or 93.6 C, corresponding suspensions rapidly lose their viability, but this loss is retarded by a hydrostatic pressure of 600 atmospheres. The rate of decrease in the number of viable spores does not conform to the kinetics of a first order reaction but exhibits a pronounced lag. In greatly diluted salt solution, disinfection at these temperatures is much faster and the lag less pronounced, but pressure retards the rate and the shape of the curves is generally similar.

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Contribution No. 407

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DICYEMA SULLIVANI, A NEW MESOZOAN FROM LOWER CALIFORNIA*

Bayard H. McConnaughey

The Dicyemidae from American waters have long remained unknown, the only published references to them being two short preliminary papers by Wheeler (1897, 1899), two by McConnaughey (1938, 1941) and part of the recent monograph by Nouvel (1947). For the past two years the writer has been engaged in a study of the dicyemids at the Scripps Institution of Oceanography, La Jolla, California. The results are embodied in a Ph.D. thesis submitted to the University of California (McConnaughey, 1948). In this work twelve species of dicyemids, including four belonging to the genus *Dicyema,* from the California coast are described.

A paper containing keys, descriptions and figures for these species has been submitted for publication. Subsequent to the preparation of this article, an additional species has been found in a small octopus from Lower California.

Dicyema sullivani n.sp.

Diagnosis: Adult nematogens usually from three-fourth to one and one-half millimeters long, slender, of about the same width throughout or with a moderate cephalic swelling broadest at the level of the paraporal cells; total number of somatic cells 28 to 33, most commonly 32; trunk very uniform in appearance, without verruciform cells or heavy accumulations of granules, the cells disposed partly in opposed pairs, partly in whorls of four; cephalic swelling darker staining than the trunk; calotte orthotropal, conical, tapering somewhat to the bluntly rounded anterior end; propolar cells about two-fifths to one-half the size of the metapolar cells; parapolar cells shield shaped, about equal in length to the length of the calotte; axial cell ending bluntly between the bases of the metapolar cells, not extending forward to the propolars.

The vermiform larvae attain a length of about 100 microns before escaping from the parent nematogens. In them the calotte is elongated, pointed, and appears to be twisted spirally a quarter of a turn so that the cells often appear to be diagonal in position (figs. 6 and 7). The axial cell ends anteriorly near the posterior ends of the metapolar cells. The first axoblasts divide early in this species so that typically four or even more are present in the larva before its escape. The axoblasts tend to remain contiguous for some time both in the larvae and in young nematogens, often forming small clusters of cells.

The axial cell nucleus may give rise by amitotic division to one or two additional nuclei, usually smaller (fig. 1).

Host: *Octopus bimaculatus* Verrill.

Distribution: At present known only from the northern part of Lower California.

Type specimens: Syntypes on slide L-14,-2, author's collection. Paratypes on some of the other slides of the L-14 series.

This species was found in one of five immature octopuses weighing from three-

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fourths to two and one-half grams, collected on a rocky flat near Rosarita Beach, Mexico, in the intertidal zone. All five of them contained nematogens of *Dicyemennea california* McConnaughey, 1941, one of them being infected in addition with the species here described. The two species were located in separate clusters on the kidney lobules, not being randomly intermixed. Only the primary nematogen phase of both species was present.

This species differs from the majority of its congeners in the fact that the axial cell terminates at the posterior end of the calotte rather than penetrating forward between the metapolar cells to the propolar cells. The other species of *Dicyema* known to exhibit this condition (*D. acheroni* and *D. acciaccatum* McConnaughey, in press, and *D. monodi* Nouvel, 1934, and *D. acuticephalum* Nouvel, 1947) are all smaller with a lower somatic cell count, and they also differ in the size and shape of the calotte and trunk.

SUMMARY

Dicyema sullivani from Lower California, a parasite of *Octopus bimaculatus* is described. Its most distinctive features are the ending of the axial cell at the posterior border of the calotte, the large somatic cell count and the early multiplication of axoblasts in the vermiform larvae.

This brings to 13 the number of species of dicyemids known to occur along the west coast of North America, 5 of them belonging to the genus *Dicyema,* 7 to *Dicyemennea* and 1 to *Conocyema.*

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EXPLANATION OF THE PLATE

All figures made with the aid of a camera lucida from preparations fixed in Bouin's fluid and stained with Ehrlich's acid hematoxylin.

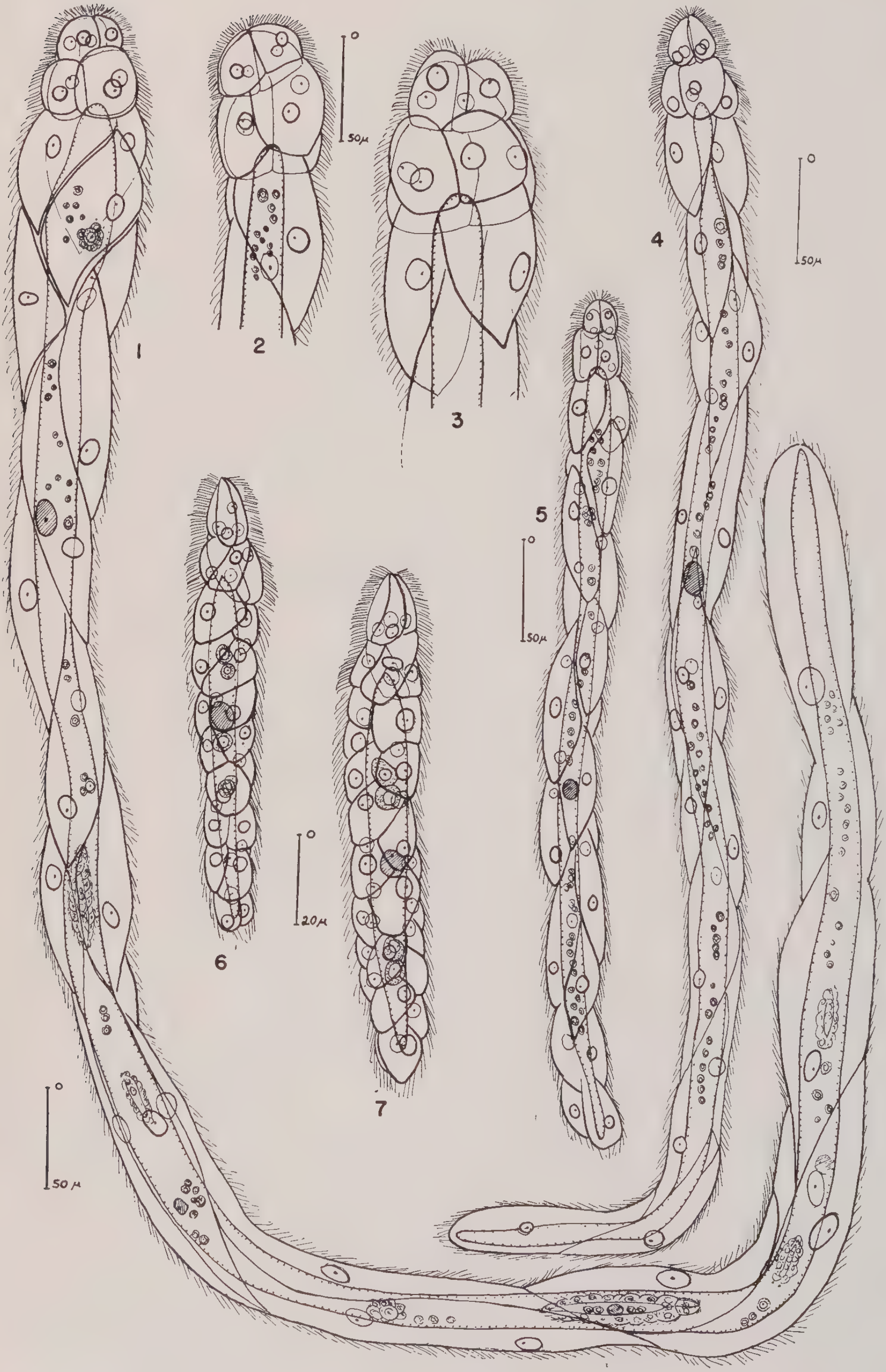
FIG. 1 Nematogen containing vermiform larvae in various stages of development. The axial cell nucleus and two small accessory nuclei present in the axial cell are hatched to distinguish them from the somatic cell nuclei.

FIG. 2. Anterior end of a nematogen in side view, showing the calotte and parapolar cells.

FIG. 3. Anterior end of a nematogen in dorsal view.

FIGS. 4 and 5. Very young emerged nematogens prior to the formation of vermiform larvae.

FIGS. 6 and 7. Vermiform larvae still inclosed in the axial cells of their parent nematogens. Note the spiral twist of the calotte, and the four axoblasts already present in the axial cell. One of the larvae has 31 somatic cells, the other 33.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Contribution No. 408

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VARIABILITY IN DIRECTION OF WAVE TRAVEL*

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Introduction

A usual assumption in wave forecasting is that the waves in a fetch travel in a uniform direction coincident with that of the wind. Aerial photographs of wave trains (FIGURE 1) and visual and instrumental observations show a complex pattern of short-crested waves with waves of appreciable height traveling not only in the wind direction, but also in other directions.

In this paper, the assumption is made that, in a generating area, waves are present which are moving at various angles with the wind direction. The growth of these waves under the influence of the tangential stress and normal pressure of the wind is calculated by generalizing the relationship for wave growth developed by Sverdrup and Munk.[1]

This variability in wave direction is not confined to the waves in the generating area, but is a feature which is retained after the waves emerge from the generating area and travel as swell. Since it is assumed that the direction of travel remains unchanged once the waves are formed, the variability in swell direction is determined by the variability in direction of the waves in the generating area.

When wave trains are interrupted by islands and headlands, such variability in the direction of wave travel is generally of greater importance in determining wave conditions in the sheltered region than refraction or diffraction. It is of critical importance in connection with longshore currents and problems of wave generation in small bodies of water of irregular shape.

Theory

Notation:

θ—angle between wind direction and direction of wave travel;
C—phase velocity of wave;
E—mean total energy of wave per unit area;
x—horizontal distance coordinate;
t—time;
R_T—mean rate of energy transfer to wave due to tangential wind stress;
R_N—mean rate of energy transfer to wave due to normal wind pressure;
U—wind velocity at about 8 m above sea surface;
ρ—density of water (1.025 g/cm^3);

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† The writer is very much indebted to Mr. C. P. Ho for his assistance and suggestions in carrying out the numerical phases of this work.

ρ'—density of air (1.25×10^{-3} g/cm^3);
γ^2—resistance coefficient applicable to wind ($\gamma^2 = 2.6 \times 10^{-3}$ for $U > 5$ m/sec);
A—$2\gamma^2\rho'/\rho$ (6.35×10^{-6});
g—acceleration of gravity (980 cm/sec^2);
s—sheltering coefficient;
α—$s/2\gamma^2$;
H—wave height (from crest to trough);
L—wave length;

FIGURE 1. Aerial photograph of waves.

δ—H/L (wave steepness);
β—$C/U \cos\theta$ (wave age);
r—coefficient of energy partition;
δ_1—value of δ for $\beta = 1$;
β'—a value of β determined by the assumed δ-value for $\beta = 0$;
F—length of fetch in direction of wave travel.

The Energy Equations and Their Solutions. Assume for the equations expressing the energy budget of a train of waves, following the method of Sverdrup and Munk:

Steady state:

$$\frac{C}{2}\frac{dE}{dx} + \frac{E}{2}\frac{dC}{dx} = R_T \pm R_N \left.\vphantom{\begin{array}{l} + C < U \\ - C > U \end{array}}\right\} \begin{array}{l} + \; C < U \\ - \; C > U \end{array} \qquad (1)$$

Transient state:

$$\frac{dE}{dt} + \frac{E}{C}\frac{dC}{dt} = R_T \pm R_N \left.\vphantom{\begin{matrix}a\\a\end{matrix}}\right\} \begin{matrix} + C < U \\ - C > U \end{matrix} \tag{2}$$

Assume

$$R_T = EAg\, U^{-1}\beta^{-3} \sec^2 \theta; \quad R_N = EAg\, U^{-1}\beta^{-3}\alpha(1 - \beta)^2 \sec \theta \tag{3}$$

where, in the case of the tangential stress, the stress component in the direction of wave advance is introduced, and, in the case of the normal pressure, the wind component in the direction of wave advance is introduced.

The solutions of the energy equations are obtained in exactly the same manner as that used by Sverdrup and Munk, and the details will not be repeated here. The authors just cited assume that wave steepness, δ, is a function of wave age, β, only, and proceed to evaluate certain constants which occur in a theoretically derived relationship by fitting observational data.

The further assumption is now made that approximately the same numerical relationship between δ and β holds for values of θ other than $\theta = 0°$. This requires redetermination of the constants r, α, δ_1, and β' for each value of Θ. The values of the constants for $\theta = 30°$ and $\theta = 45°$ as compared to those obtained by Sverdrup and Munk for $\theta = 0°$ are as follows:

θ	r	α	δ_1	β'
0°	0.580	2.50	0.0380	0.350
30°	0.563	3.14	0.0393	0.344
45°	0.544	4.19	0.0402	0.339

The solutions can all be presented as relations between non-dimensional ratios, and the results in such form for $\theta = 30°$ and $\theta = 45°$ are compared to those of Sverdrup and Munk for $\theta = 0°$. FIGURE 2 shows the parameters C/U and gH/U^2 plotted against gF/U^2 (F is the fetch in the direction θ), that is, wave speed and height as functions of fetch and wind velocity assuming unlimited duration. FIGURE 3 shows in terms of the non-dimensional ratios C/U, gH/U^2, and gt/U, the wave speed and height as functions of duration and wind speed, assuming unlimited fetch.

Discussion

In determining the height and period of waves traveling in a direction other than the wind direction, it is convenient to make use of the ratios H_θ/H and T_θ/T, where H_θ and T_θ are the height and period respectively of the waves traveling over a distance F at an angle θ to the wind direction, and H and T are the corresponding height and period of the waves traveling *with* the wind over the same distance. The distance F is measured in the direction θ. An alignment chart (FIGURE 4) gives H_θ/H and T_θ/T as functions of wind velocity U, and either fetch F (steady state) or duration time t (transient state) for θ equal to 30° and 45°. An example is shown.

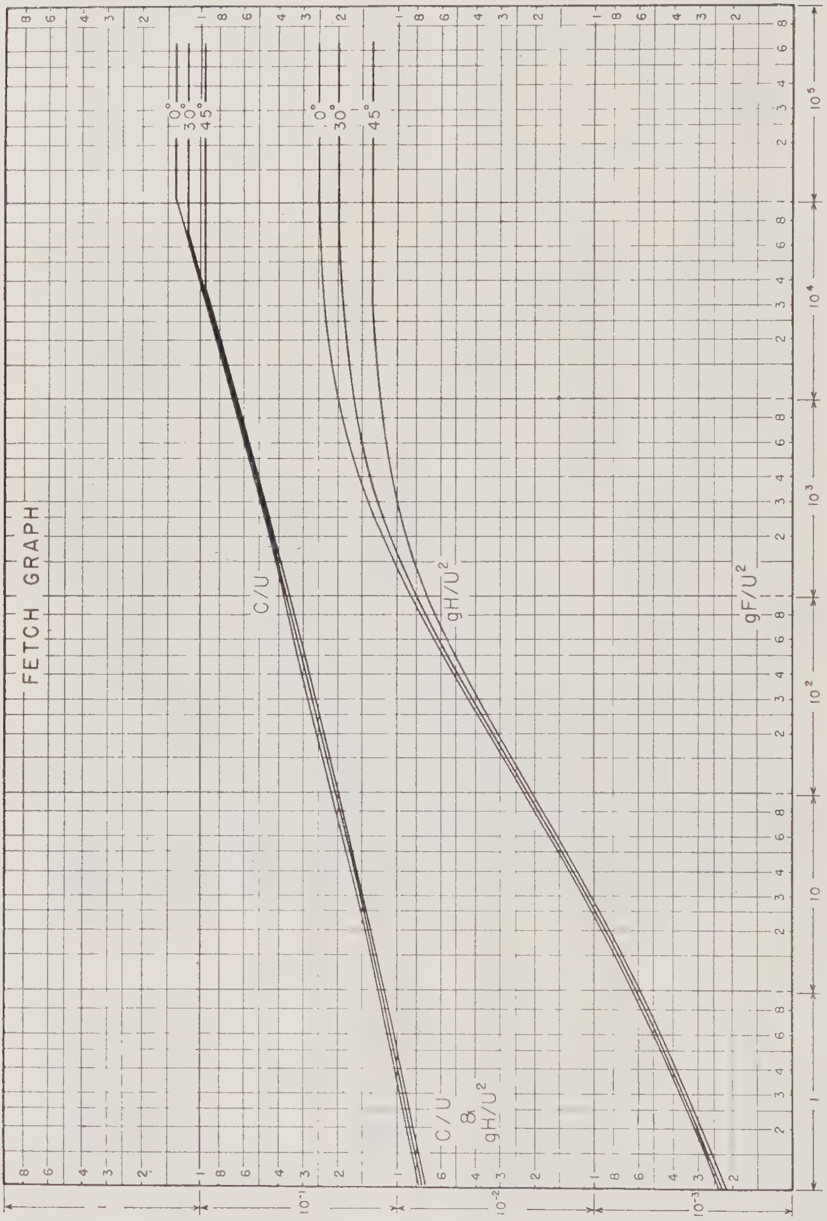

FIGURE 2. Curves giving wave velocity and wave height as functions of fetch and wind velocity in terms of non-dimensional parameters for angles of 0° (after Sverdrup and Munk), 30°, and 45°.

In order to determine H_θ and T_θ, it is first necessary to find H and T by means of Plates I and II of Scripps Institution of Oceanography Wave Report No. 73,[2] or from the non-dimensional representations for $\theta = 0_\theta$. The question as to the existence of a steady state or transient state in the fetch is settled at the same time. H_θ/H and T_θ/T are then determined from FIGURE 4 and a simple multiplication gives H_θ and T_θ. The modification of H_θ and T_θ as the waves decay through a certain distance D is determined by means of the decay diagram[1, 2].

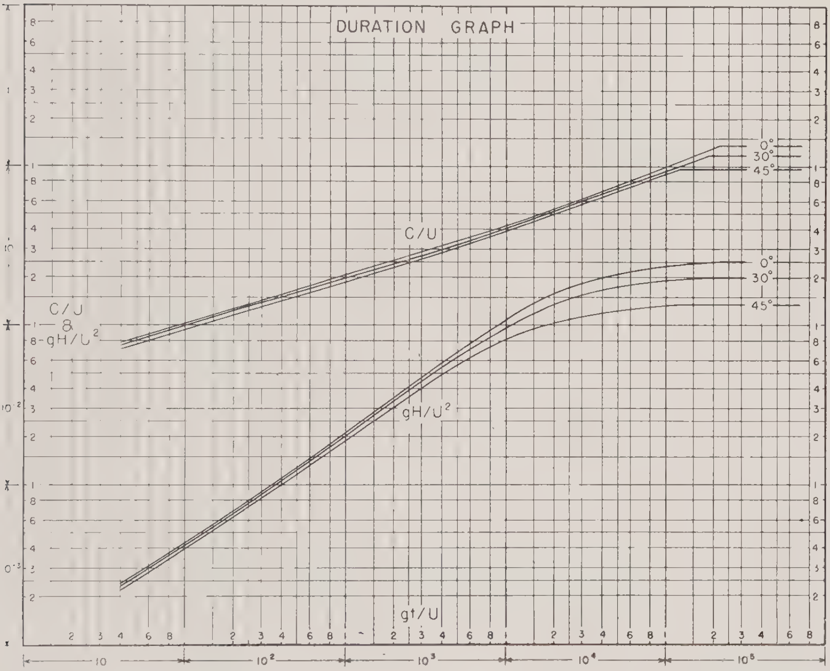

FIGURE 3. Curves giving wave velocity and wave height as functions of duration time and wind velocity in terms of non-dimensional parameters for angles of 0° (after Sverdrup and Munk), 30° and 45°.

FIGURE 4 shows that as the angle θ increases, the wave height and period decrease. The percentage decrease is less for higher wind velocities, and is less for period than for height. The waves moving at an angle of 30° with the wind have heights between 80 per cent and 90 per cent of those moving with the wind for typical values of the forecasting parameters. For 45°, the heights are between 55 per cent and 75 per cent. Since waves of different heights are present in the fetch, it is to be expected that the higher waves which travel more nearly in the direction of the wind shelter the lower waves. FIGURE 4 therefore may be expected to give values of H_θ somewhat too large for small values of the ratio H_θ/H. No adequate observations are available from which a quantitative estimate of the effect may be made. Relationships for θ larger than 45°, have not been reproduced for this reason.

The present analysis assumes that, in a fetch, waves are moving in every direction which does not deviate from the wind direction by more than 45°. Since the wind can transfer only a finite amount of energy to wave

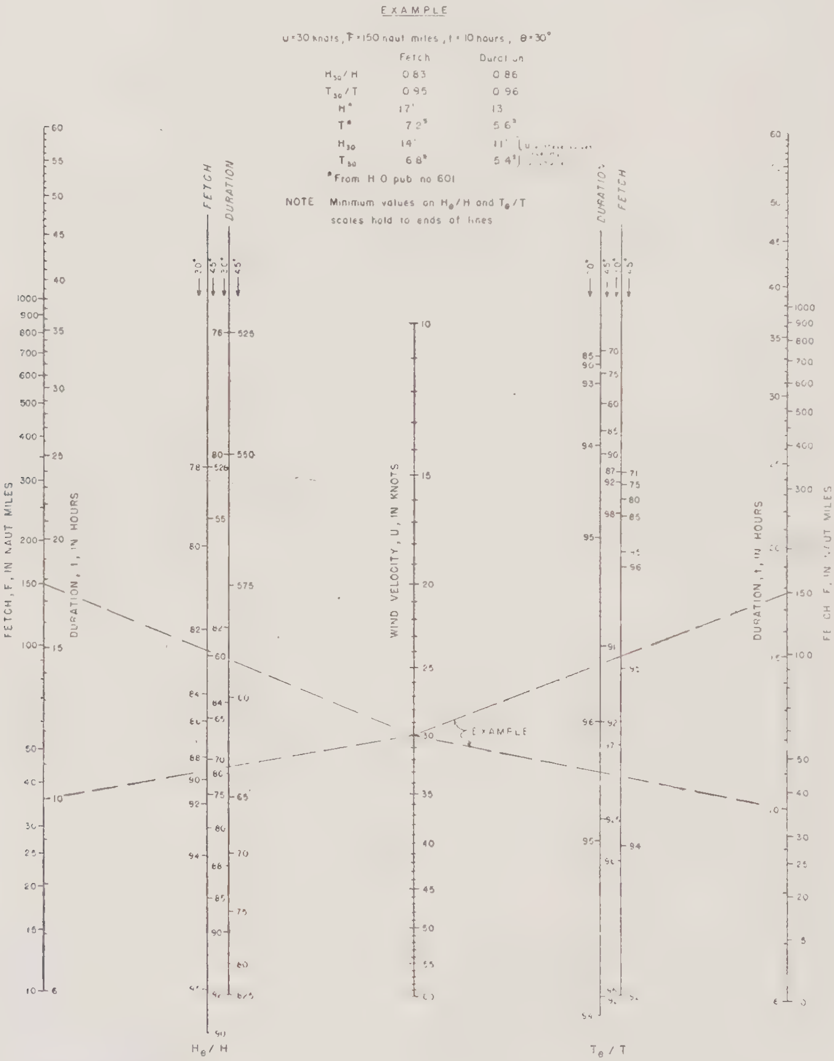

FIGURE 4. Alignment chart for the computation of height and period of waves moving at angles of 30° and 45° with the wind.

growth, the waves moving in a given direction must show height and period variability with time. The quantities H_θ and T_θ may be expected to apply to waves which correspond to the "significant waves" discussed by Sverdrup and Munk.[1] It is to be noted that the frequency distribution of the wave height and period spectra may change with the angle θ.

Application

Comparison with Forecasting Experience. Forecasting experience[3] has demonstrated the need for considering that waves decaying from a fetch where wind direction is uniform reach not only points in line with the wind (A of FIGURE 5), but also those at angles up to 30° (B of FIGURE 5). The same height and period values have been used regardless of angle. This practice is in rough agreement with the variability results discussed above, since, for θ less 30°, the value of H_θ/H is generally greater than 0.80, and T_θ/T is greater than 0.95.

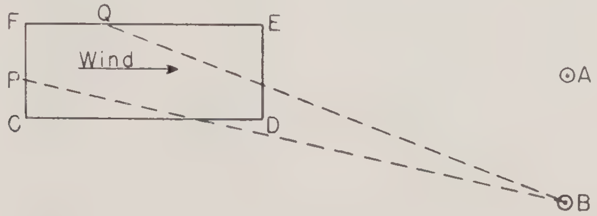

FIGURE 5. Schematic representation of a fetch area CDEF from which waves arrive at points A and B.

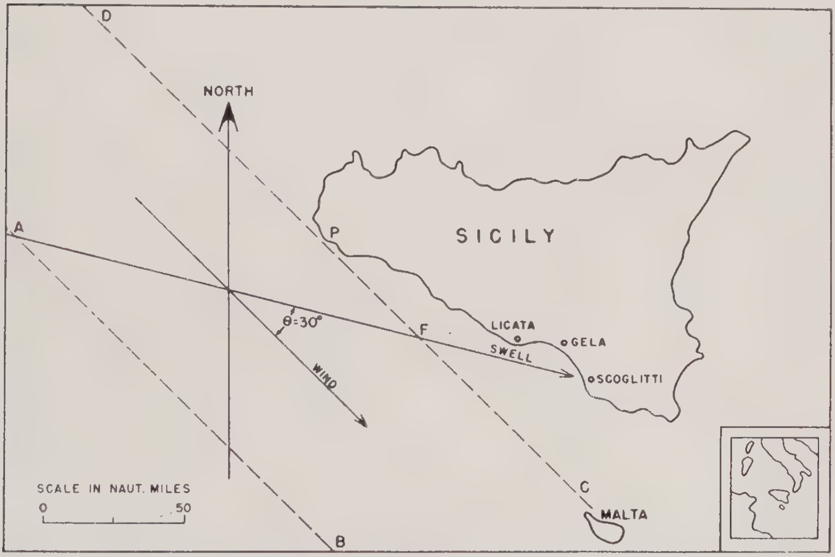

FIGURE 6. Origin of swell at the Scoglitti beachhead during the invasion of Sicily.

Invasion of Sicily. Data from a report on the invasion of Sicily[4] can be used to make a check on the theory. The weather maps show that any swell affecting the landing near Scoglitti must have been generated in region ABCD (FIGURE 6) by the north-northwest to northwest winds whose velocities were as high as 31 knots up to 2000 GCT, D-1 day. The winds in the region to the east of line CD and south of Sicily were also from the northwest but velocities were less than 16 knots, because of the sheltering effect of the island. The only swell which could approach the beach at Scoglitti would be that refracted or diffracted from point P, at the southwest corner of the island, or that proceeding from region ABCD as a result of variability in direction of travel. Because of the bottom topography and the distance involved, the "refraction factor"[5] associated with waves refracted from P to Scoglitti would be very small. Diffraction studies show that the "diffraction factor"[6] would also be very small. However, relatively high swell would be expected off Scoglitti as a result of variability in direction of travel of waves generated in area ABCD. The highest swell to be expected would be generated over a path AF with θ equal to 30°. The computation of height for point F of waves moving at an angle of 30° to the wind is as follows:

F	U	t*	H	θ	H_θ/H	H_θ
150 miles†	30 knots	10^h	13′	30°	0.86	11′

A following wind is present as the waves decay a distance of about 50 miles from point F to Scoglitti. It is assumed that the following wind is sufficient to keep the swell from decreasing in height over the decay distance. As a result, the expected height of the swell off the beach at Scoglitti would be 11 feet. The travel time would be about 5 hours so that the swell would arrive at approximately H-hour. Observations during the early landings showed a swell height of 10 to 12 feet.

San Clemente Island. Observations of wind waves were made around the southern end of San Clemente Island, California, on June 30, 1947 from the E. W. SCRIPPS, research vessel of the Scripps Institution. Stations A and B (FIGURE 7) were occupied at 0618 and 0730 PST respectively. Other stations to the east of the island were also occupied to determine the island's effect on westerly swell, but no swell was discernible on this occasion. The wave data (FIGURE 7) were obtained by visual observation of a short-line-spar buoy wave meter.

Station A is exposed to waves generated in the fetch to the northwest by the winds which at this season are predominantly northwesterly. This fetch is interrupted by San Nicholas Island, 50 miles to the northwest, and the Santa Barbara Islands, 100 miles to the northwest. However, a small change of angle gives an unobstructed fetch. Assuming steady state conditions, the following values of the forecasting parameters are consistent with the observed height and period at Station A:

Wind Direction	U	F	Wave Direction	θ
NW	14 knots	250 miles	NW	0°

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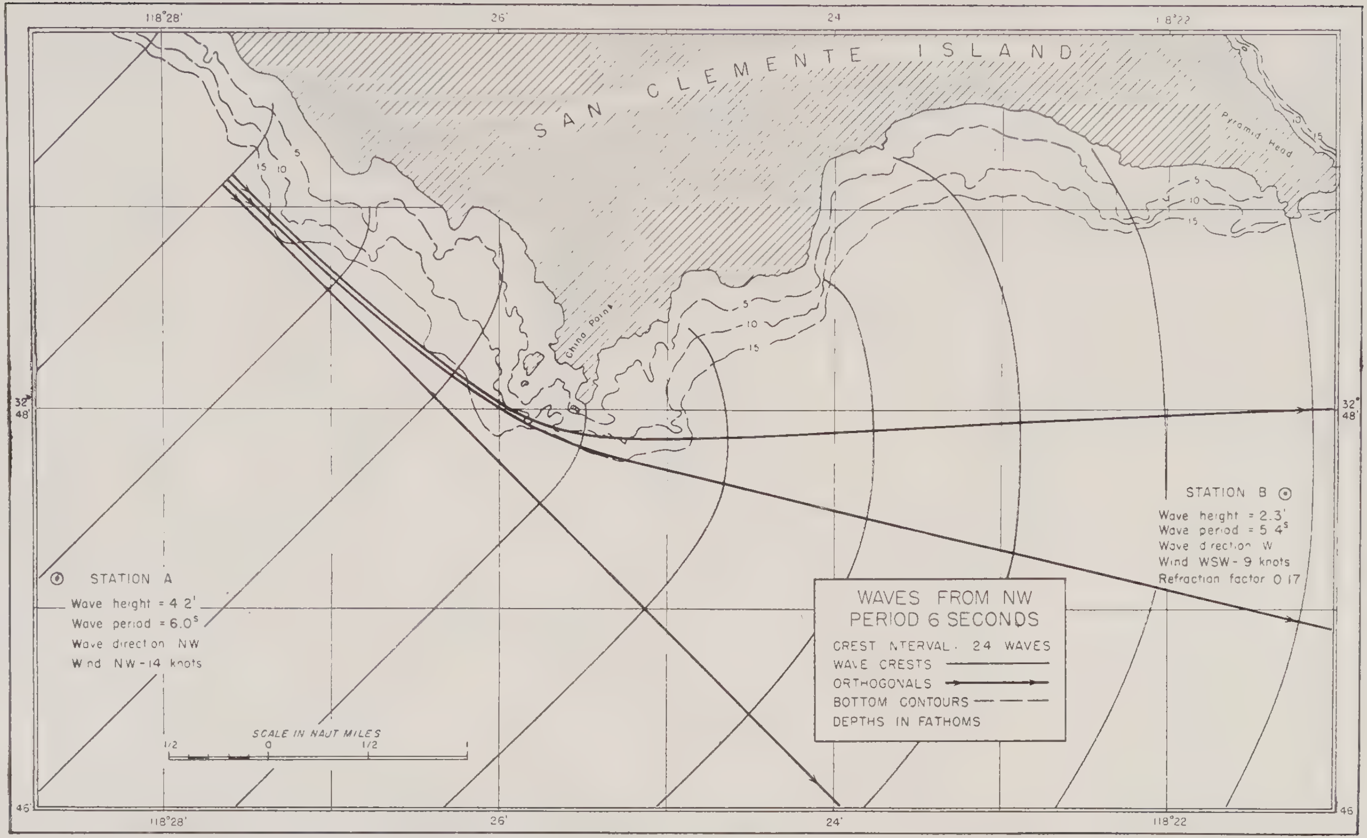
* The actual duration time of the high wind velocities has been extended to allow for the waves already present in the fetch.[3]

† All miles referred to are nautical miles.



118°28'
26'
24
118°22
SAN CLEMENTE ISLAND
Pyramid Head
China Point
5
10
15
32°
48'
46'
STATION B
Wave height = 2.3'
Wave period = 5.4s
Wave direction W
Wind WSW - 9 knots
Refraction factor 0.17
STATION A
Wave height = 4.2'
Wave period = 6.0s
Wave direction NW
Wind NW - 14 knots
WAVES FROM NW
PERIOD 6 SECONDS
CREST INTERVAL · 24 WAVES
WAVE CRESTS
ORTHOGONALS
BOTTOM CONTOURS
DEPTHS IN FATHOMS
SCALE IN NAUT MILES
1/2
0
1/2

FIGURE 7. Refraction diagram for China Point region, San Clemente Island, with wind wave observations for both a sheltered and unsheltered station.

Because of China Point, waves can reach Station B only from due west or southerly directions. In view of the wind field, the waves observed at Station B must be a result of refraction or diffraction at China Point, or variability in direction in the northwesterly fetch. Since the refraction coefficient is 0.17 and the diffraction coefficient is less than 0.10, these processes cannot account for the observed waves at B. The maximum height as a result of variability in direction would be associated with waves from the west. The computation of these waves from the above forecasting parameters is as follows:

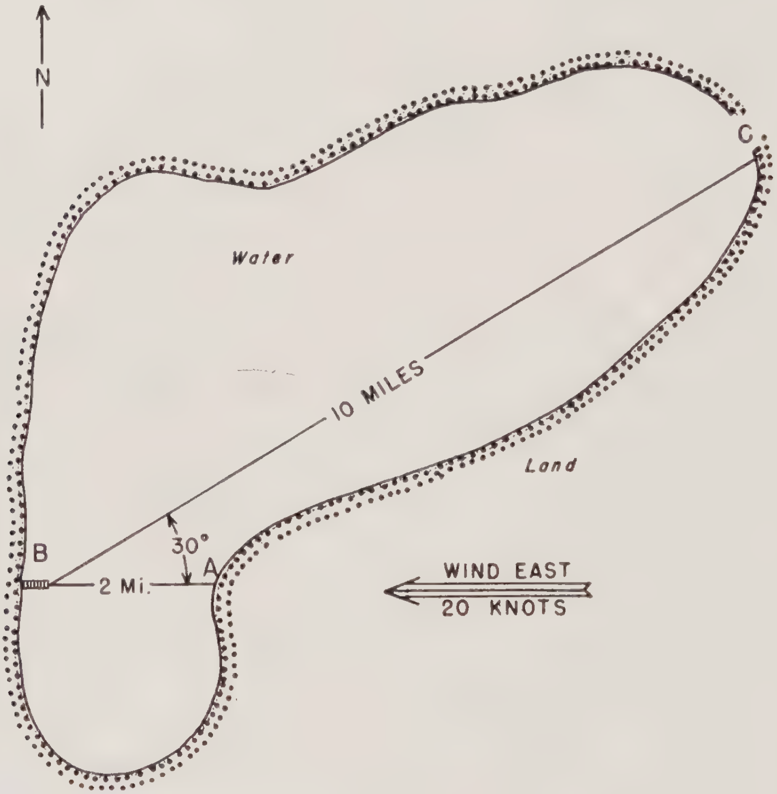


FIGURE 8. Schematic diagram illustrating the "direct" fetch, AB, and the "effective" fetch, CB, for waves reaching point B in a small body of water of irregular shape.

θ	H_θ/H	T_θ/T	H_θ	T_θ
45°	0.55	0.76	$0.55 \times 4.2 = 2.3'$	$0.76 \times 6.0 = 4.6^s$

The values compare favorably with the observed height of 2.3 feet and period of 5.4 seconds.

Conclusions

The present results indicate that, within the fetch, waves may be expected to grow, even though they are moving at angles of as much as 45° with the wind direction. The height of such waves will be at least 50 per cent of the height of waves moving with the wind. Within the fetch ,the waves moving with the wind or at small angles to the wind appear dominant, but waves moving at larger angles are important when a wave train is interrupted by an island or headland. Variability in direction of swell can be determined by considering the different paths in the fetch which are directed toward the point where swell is to be considered. Lines PB and QB in FIGURE 5 represent two such paths. Variability in direction of swell may be expected to decrease with increasing decay distance.

FIGURE 8 illustrates schematically a critical case in connection with variability in a body of water of irregular shape. Assuming steady state conditions, the waves reaching point B from along the "direct" fetch AB have computed heights of 1.5 feet, whereas those reaching B from along the "effective fetch" BC have computed heights of 3.5 feet. No checks have been made on the application of the principles given here to small bodies of water, and it is recommended that the results be used only as a guide until such checks have been made.

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Discussion of Paper

DR. W. L. DONN (*Brooklyn College, Brooklyn, N. Y.*): In the course of studying wave and swell records for the Woods Hole Oceanographic Institution, with the purpose of correlating swell observations with marine weather conditions off the eastern coast of the United States, certain inexplicable discrepancies were noted which appear explainable in the light of the wave variability theory.

The records were made by a bottom-resting, pressure-type wave meter, about a mile southeast of Cuttyhunk Island, near the western end of Cape Cod. The meter was constructed and operated by the Woods Hole Oceanographic Institution. The weather correlation was attempted on the basis of the North Atlantic Weather Maps prepared by the U. S. Weather Bureau at La Guardia Field, Long Island.

The exposure of the wave meter was such that the only "window" for the free approach of waves from a distant source was from a sector bounded by lines extending to the southeast and southwest. A fetch of but a few miles of shoal water exists to the north and northwest of the recording station. To the west and west-southwest, in the directions of Long Island Sound and Long Island respectively, a possible fetch of more than 100 miles occurs, with water depths averaging close to 20 fathoms.

Most of the significant swell recorded on the Cuttyhunk meter (periods from 6 to 10 seconds) could be correlated with synoptic situations in which cyclonic warm sectors existed off or along the eastern coast. In such cases, the southerly or southwesterly winds which prevailed had a relatively long fetch along the coastal waters. The duration of these winds was normally closed with the passage of a cold front. The strong northwesterly winds which followed the fronts rapidly damped the pre-existing southerly swell.

In certain cases, with strong west to west-northwest winds following the frontal passage, the wave records either did not show the expected damping, or showed new waves developing of the same order as those previously existing. This was difficult to explain in view of the up-wind fetch being limited to a few miles by the coastline of Connecticut. However, if a deviation of wave propagation from wind direction of 30 degrees is permitted, the effect of the strong winds over the longer fetch to the west and west-southwest, mentioned above, might have permitted the development of the observed waves.

These observations appear explainable from qualitative considerations, although more complete quantitative studies will be made to check the observations further.

Contribution No. 409

NOTE ON PERIOD INCREASE OF WAVES*

BY WALTER H. MUNK

IN A previous paper[1] the author derived the expression

$$\frac{dT}{dx} = \left(\frac{1}{C} - \frac{1}{V}\right) \frac{\partial T}{\partial t} \tag{1}$$

for the increase in period T of an individual wave the identity of which was conserved over a distance x. Here, V represents group velocity, C wave velocity, and $\partial T/\partial t$ the rate of period decrease at a fixed point. The equation was applied to the tsunami of April 1, 1946, and the Mexican earthquake of February 22, 1943.

Wilson's application.—Recently, Wilson[2] applied equation (1) to Love waves of the South Atlantic earthquake of August 28, 1933, for which identification of individual waves is more definite than in the example used by the author. Wilson derives the group and wave velocities from the equations

$$\tan\left[kh\sqrt{(C^2/V_1^2) - 1}\right] = \frac{\mu_0}{\mu_1} \frac{\sqrt{1 - (C^2/V_0^2)}}{\sqrt{(C^2/V_1^2) - 1}} \tag{2}$$

$$V = C + kC' \tag{3}$$

where V is the velocity of shear waves and μ the rigidity, the subscripts "one" and "zero" referring to an upper layer of thickness h, and a lower layer of infinite thickness, respectively; where $L = 2\pi/k$ is the wave length, and where $C' = dC/dk$, the prime thus designating differentiation with respect to k. Using the numerical values

$$\begin{aligned} V_1 &= 4.0 \text{ km/sec.}, & \mu_0/\mu_1 &= 1.4, \\ V_0 &= 4.5 \text{ km/sec.}, & h &= 22 \text{ km.}, \end{aligned} \tag{4}$$

Wilson obtains good agreement with observations. The use of theoretical equa-

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* This work represents the results of research carried out for the Office of Naval Research the Hydrographic Office, and the Bureau of Ships of the Navy Department, under contract with the University of California. Manuscript received for publication July 12, 1948.

[1] W. H. Munk, "Increase in the Period of Waves Traveling over Large Distances; with Applications to Tsunamis, Swell, and Seismic Surface Waves," *Trans. Am. Geophys. Union,* 28: 198–217 (1947).

[2] James T. Wilson, "Increase in Period of Earthquake Surface Waves with Distance Traveled," *Bull. Seism. Soc. Am.*, 38: 89–93 (1948).

tions for V and C represent a marked improvement over the author's method[3] of determining V and C from empirical data. From the foregoing equations and numerical values Wilson computed

$$dT/dx = 2.3 \times 10^{-3}\ \text{sec/km.}, \tag{5}$$

which is not inconsistent with the observed data (fig. 1).

Eckart's equations for the wave front.—Equations (1) and (2) are based on the assumptions of periodic, sinusoidal waves. These assumptions cannot be expected to lead to satisfactory approximations near the wave front, the portion of the record with which Wilson and the author mainly have been concerned, where the wave length changes appreciably from wave to wave. A more suitable approximation, involving the Airy integral, has been discussed recently by Jeffreys,[4] Pekeris,[5] and Eckart.[6] Let the subscript "zero" refer to the limits reached as the wave length becomes infinite ($k = 0$). Assuming centered waves the group velocity of which reaches a maximum, V_0, for $k = k_0 = 0$, Eckart obtains for the disturbance in the neighborhood of the wave front

$$\psi = \frac{\phi_0}{\delta} Ai(\Delta/\delta) \tag{6}$$

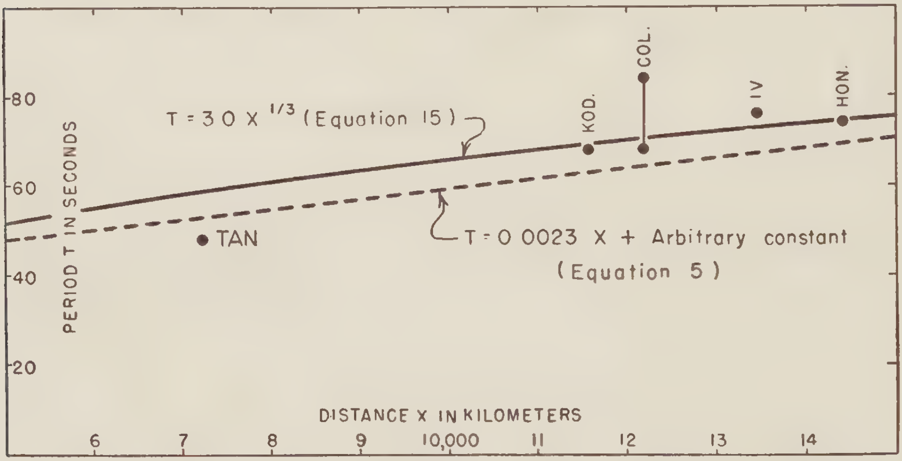

Fig. 1. Comparison between computed and observed wave periods. The observations and dashed lines are according to Wilson. The theory for the solid line follows from Airy's integral.

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[3] Munk, *op. cit.*

[4] H. Jeffreys and B. S. Jeffreys, *Methods of Mathematical Physics* (Cambridge University Press, 1946), pp. 483–486.

[5] C. L. Pekeris, "Theory of Propagation of Explosive Sound in Shallow Water," *Geol. Soc. Am., Memoirs*, No. 27 (1948).

[6] C. Eckart, "The Approximate Solution of One-Dimensional Wave Equations," *Rev. Mod. Phys.*, 20: 399–417 (1948).

where $\phi(k)$ is the amplitude spectrum of the waves, essentially determined by the initial disturbance, where $Ai(z)$ is the Airy function (fig. 2),

$$\delta = -(\tfrac{1}{2} V_0'' t)^{1/3} \tag{7}$$

is a scale factor, and

$$\Delta = x - V_0 t \tag{8}$$

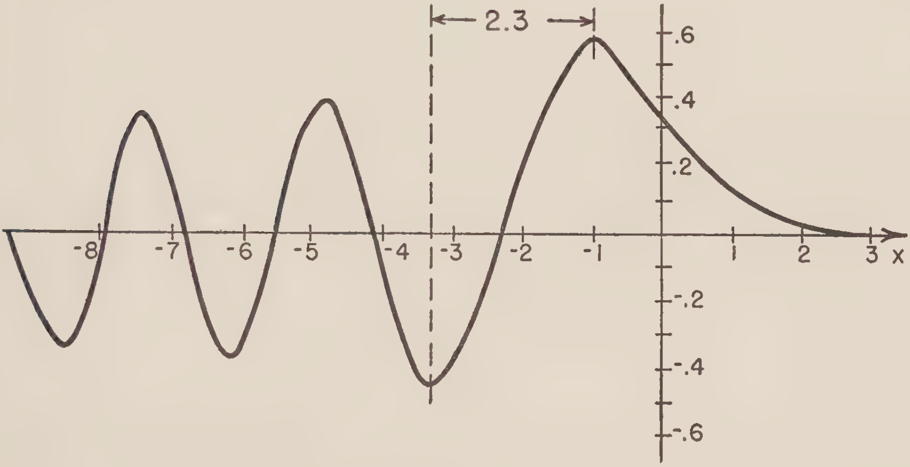

Fig. 2. Graph of the Airy function, $Ai(z)$, from Eckart.

is the distance from the wave front. Near the wave front ($\Delta << x$) the disturbance is determined by the oscillation of the Airy integral, and the wave length can be computed by reading values from figure 2. The distance between the first crest and trough equals

$$\tfrac{1}{2} L = 2.3\,\delta\,, \tag{9}$$

and *the wave length increases as the cube root of time*, as pointed out by Eckart.[7]

Application of the Airy integral to Love waves.—Near the wave front, where, according to (2) and (3)

$$C \doteq V \doteq V_0\,, \tag{10}$$

equations (9) and (10) combined with $C = L/T$ and $x = V_0 t$ give

$$T = \frac{-4.6\,(\tfrac{1}{2} V_0'' x)^{1/3}}{V_0^{4/3}} \tag{11}$$

---

[7] *Op. cit.*

for twice the time interval between the first crest and trough (or trough and crest). This is the definition of period used by Wilson in figure 1. *The wave period near the front increases, therefore, as the cube root of travel distance.*

Successive differentiation of equation (2) gives

$$V'' = 3C'' + kC''', \qquad V_0'' = 3C''. \tag{12}$$

In view of the approximation implied by (10) one obtains from equation (2)

$$C'' = -V_0\left(\frac{h\mu_1}{\mu_0}\right)^2\left(\frac{V_0^2}{V_1^2} - 1\right)^2, \tag{13}$$

which, when combined with (11) and (12), gives

$$T = 4.6\left(\frac{3}{2}\right)^{1/3} V_0^{-1}\left(\frac{h\mu_1}{\mu_0}\right)^{2/3}\left(\frac{V_0^2}{V_1^2} - 1\right)^{2/3} x^{1/3}. \tag{14}$$

For the numerical values given in equation (4)

$$T = 3.03\,x^{1/3}, \tag{15}$$

where T is in seconds and x in km. According to figure 1, the computed wave periods compare favorably with the measured periods. The slopes of the two lines are very nearly equal, indicating that equation (1) applies near the wave front to a surprising degree of accuracy. Equation (15) has the advantage over equation (1) that it *does not involve an arbitrary constant, but that it gives a complete solution* $T(x)$ *in terms of the properties of the transmitting medium.* It may offer a means for determining the thickness of the upper layer if the velocities of the shear waves and rigidities of the layers are known.

Application to ocean swell.—The author wishes to use this opportunity to point out an error in his previous paper.[8] Equation (1) refers to the period increase of individual waves. Its application depends, therefore, upon the possibility of identifying and tracing individual crests between stations. This is sometimes possible with respect to such slightly dispersive waves as tsunamis and early Love waves; it has not been possible with respect to swell. Accordingly, when we speak of an increase in the period of swell with distance from the storm area, we do not mean the period of individual waves, but rather the period associated with maximum energy in the frequency spectrum of the waves. These are the most prominent waves present, and the increase of their period with travel distance has definitely been established by observations. Equation (1) for the period increase of individual waves has no bearing upon this problem; the explanation must be sought in selective attenuation, such as results from the air resistance against the traveling swell.[9]

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[8] Munk, *op. cit.*

Thus the problem of period increase falls into two separate problems, and much of the confusion has resulted from failure to distinguish between these two. If the wave period is defined as the time interval between two crests that can be traced between stations, then the explanation is a kinematic one, involving equation (1), or, very near the wave front, special solutions such as equation (14). If by wave period is meant the period associated with an energy maximum in the frequency spectrum, then the explanation must be sought in some mechanism involving selective attenuation.

---

[9] H. U. Sverdrup, "Period Increase of Ocean Swell," *Trans. Am. Geophys. Union*, 28: 407–417 (1947).

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THE REALITY OF REGULARITIES INDICATED IN SEQUENCES OF OBSERVATIONS

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SUPPOSE THAT A SEQUENCE of observations exhibits a striking regularity; for example, suppose that the values arrange themselves in their order of magnitude, either increasing or decreasing, or that they indicate a maximum or a minimum. Is the indicated regularity real, is it true of the sequence or statistical set sampled, or is it the result of sampling from a random sequence? That is if the process were repeated, is there reason to believe that approximately the same general result would recur? The more improbable it is that the indicated regularity could have arisen as a result of random sampling, the greater is the justification for regarding the indications of the sample as truly representative. Unless the probability of obtaining an indicated regularity is small, there is no evidence of the existence of an actual regularity of the indicated type.

First, assuming that only the sequence of individual numerical quantities is available, we may apply various tests based upon characteristics of a random sequence (see Besson, 1920; Clough, 1921, 1924; Crum, 1921; Woolard, 1925; Working, 1934; Kermack and McKendrick, 1936–37; as well as a series of later and more exhaustive contributions). For example, the number of maxima in a sequence of unrelated numbers is one-third of the number of terms. The departure of a sequence in any characteristic from that deduced for a random sequence suggests some systematic influence, and the evidence in favor of such an influence depends upon the extent of the departure and the number of terms. In general, such laws of chance sequences do not serve as criteria for proving the presence of some systematic influence, unless there are a large number of terms. Moreover, the results of attempting to determine the probability of obtaining a short sequence of terms having a striking appearance of regularity tend to be rather misleading.

Second, form a sequence of averages of groups of individual observations selected from a given sequence in a known systematic way. For example, a sequence might be repeated any number of times. Then averages of corresponding terms would form a composite sequence to be tested. The statistical significance of such a sequence of averages may be determined by comparing the variance of the individual observations computed directly with that derived from the variances of the averages. This analysis of variance principle can be extended to the general case in which values of the dependent variable are related to each of a number of correlated independent variables. In this problem of multiple curvilinear correlation a sequence of averages of the dependent variable can be computed corresponding to each independent variable, and corrected to constant values of the other independent variables. A method is devised for testing the statistical significance of each such sequence of averages, as well as the composite significance of all of the sequences.

REALITY OF AN INDICATED REGULARITY OF AVERAGES CORRESPONDING TO VALUES OF ONE INDEPENDENT VARIABLE

Frequently the values in a sequence are averages of measurements or numbers grouped in some systematic way. Statistical methods have been derived for calculating probabilities in such cases and depend upon the variability between the averages and within the groups. For practical purposes readily applicable methods are needed for determining such probabilities, and approximate estimates are acceptable. Investigations of the special case where the indicated regularities of a sequence are periodic are presented in numerous publications following the pioneer work done by Schuster and Buys-Ballot before 1900 (see Alter, 1927, 1933; Chree, 1924; Cox, 1923, 1924; Dodd, 1927; Kuznets, 1919; Powell, 1930; Stumpff, 1925, 1937; Walker, 1930).

The standard deviation of the group means multiplied by the square root of the number of observations used in computing a mean is one estimate of the standard deviation of the entire series, which may also be computed directly. Let

m = number of columns or groups
n = number of entries per column
$\bar{y}_s$ = a group mean
$\bar{y}$ = the grand mean

Then, if the entire arrangement is assumed to be accidental,

$$\sqrt{n}\,\sigma_n = \sqrt{n}\left[\sqrt{\frac{\sum(\bar{y}_s-\bar{y})^2}{m}}\right]$$

should not differ from

$$\sigma_0 = \sqrt{\frac{\sum(y-\bar{y})^2}{mn}}$$

by more than would be expected from sampling errors. Using this principle, Cox (1924) employed the following criterion of significance, often used by engineers and meteorologists. If the accidental error of σ_0 is assumed to be relatively small, the standard error of the ratio $\frac{\sqrt{n}\sigma_n}{\sigma_0}$ should be proportional to that of σ_n. He used the approximation $\sigma_n/\sqrt{2m}$ for this standard error. Accordingly, he compared the difference $\left[\frac{\sqrt{n}\sigma_n}{\sigma_0}-1\right]$, which for a chance arrangement should on the average equal zero, with a standard error, $\frac{\sqrt{n}\,\sigma_n}{\sigma_0\sqrt{2m}}$. According to usual practice, a difference exceeding two or three times this standard error is evidence of some systematic relation between the averages. He used such a criterion for the existence of a periodic law of rainfall. This

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method is based upon the assumptions of the theory of large samples and may therefore often be inapplicable. Moreover, it would be better to compare $\sqrt{n}\,\sigma_n$ with the standard deviation of individual results from their sample means rather than with σ_0, which contains both sources of variability. This method may be improved by means of correction factors depending upon the size of the sample (E. S. Pearson, 1935). Thus for σ_n write $1/b_m\,(s)$, where s denotes the estimated standard deviation based upon m averages and, according to Pearson's table 13, $1/b_m$ has the following values:

$m =$	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	20	25	30
$1/b_m =$	1.772	1.382	1.253	1.189	1.151	1.126	1.108	1.094	1.084	1.075	1.068	1.063	1.058	1.054	1.050	1.040	1.031	1.026

In general the foregoing method, though widely used, is too uncertain and should be discarded.

The statistical significance of indicated regularities will now be considered with the aid of certain modern statistical principles whose detailed explanation can be found in the references cited. The probability that the variation between the averages of each column is due to chance may be estimated by means of the method of analysis of variance (Fisher, 1932; Tippett, 1931). An outline of the procedure follows:

m = number of columns
n_s = number of entries in column s
N = total number of entries $= \sum n_s$
y = any individual observation
$\bar{y}$ = grand mean of all the observations
a = a convenient assumed value of $\bar{y}$ to use in making computations
$h = (\bar{y} - a)$
$\bar{y}_s$ = mean of observed values in column s

$$V_s = \text{mean variance between columns} = \frac{\sum_1^{\mathrm{m}} \mathrm{n}_s(\bar{y}_s - a)^2 - Nh^2}{(m-1) = n_1}$$

$$V_r = \text{residual variance} = \frac{\sum (y-a)^2 - \sum_1^{\mathrm{m}} n_s(\bar{y}_s - a)^2}{(N-m) = n_2}$$

$$Z = \log_e \sqrt{V_s/V_r}$$

$$\left.\begin{aligned} n_1 &= m - 1 \\ n_2 &= N - m \end{aligned}\right\} = \text{degrees of freedom}$$

From Fisher (1932), table VI; Yule and Kendall (1937), appendix tables 6A, 6B, 6C; Fisher and Yates (1938), table V, read off the probability corresponding to Z and the degrees of freedom n_1 and n_2 of getting a variability between column means as great as that observed, or greater, corresponding to the variability of the individual values within the groups or columns.

Values for Z for only the 20 %, 5 %, 1 %, and 0.1 % points have been published, but results can be calculated approximately as follows for other points: If n_1 and n_2 are large or if they are approximately equal, the distribution of Z tends to approach normality, the standard deviation being (Tippett, 1931)

$$\sigma_z = \sqrt{\frac{1}{2}\left(\frac{1}{n_1}+\frac{1}{n_2}\right)}.$$

Accordingly, the probability is the complement of that in Yule and Kendall (1937), appendix table 2, or in Pearson (1930) table II, corresponding to

$$T = Z \div \sqrt{\frac{1}{2}\left(\frac{1}{n_1}+\frac{1}{n_2}\right)}.$$

An approximate method of interpolation or extrapolation, adapted to cases in which neither n_1 nor n_2 need be large, is to read off theoretical values of Z corresponding to the 20 %, 5 %, 1 %, 0.1 % points from table V, Fisher and Yates (1938). Then calculate values of T as follows:

$$\begin{aligned}
\mathrm{T} &= 0.842\ (\text{observed } Z) / (\text{theoretical } Z \text{ for } 20\,\% \text{ point})\\
\mathrm{T} &= 1.645\ (\text{observed } Z) / (\text{theoretical } Z \text{ for } 5\,\% \text{ point})\\
\mathrm{T} &= 2.326\ (\text{observed } Z) / (\text{theoretical } Z \text{ for } 1\,\% \text{ point})\\
\mathrm{T} &= 3.090\ (\text{observed } Z) / (\text{theoretical } Z \text{ for } 0.1\,\% \text{ point})
\end{aligned}$$

and read off the probability corresponding to the normal law (Yule and Kendall, 1937, appendix table 2; or Pearson, 1930, table II). The multipliers, 0.842, 1.645, 2.326, and 3.090, correspond to the correct probabilities if the observed Z equals the theoretical Z, and it is assumed that T varies in proportion to the observed Z as in the previous formula. This method gives a closer approximation as the values of n_1 and n_2 increase.

Another method of interpolation that may also provide values extrapolated somewhat beyond the tabular limits depends upon the approximate relation

$$Z = A - B \log P,$$

found empirically from the tables, where A and B are constants for given values of n_1 and n_2. Accordingly, if values of Z corresponding to any values of n_1 and n_2 are plotted on the uniform scale of semi-logarithmic paper and values of the probability P are plotted on the logarithmic scale, the probability corresponding to the observed Z may be read from a straight line between appropriate points. For larger values of n_1 and n_2 the approximate value of the probability P may be calculated from Fisher's formulas, where the functions $A(P)$, $B(P)$, and λ may be plotted from values corresponding to $P =$ 0.1 %, 1 %, 5 %, and 20 % (Fisher and Yates, 1938, table V; and the supplementary results found by Cochran, 1940). Results equivalent to Fisher (1932), table VI, are given by Snedecor (1934), table XXXV, directly in terms of the ratio $F = V_s/V_r$.

The foregoing methods of testing apparent regularities in series of observations are illustrated by numerical applications to two classes of natural phenomena, seasonal rainfall and sunspot numbers. First, consider the data, as given in table 1, on the seasonal rainfall at San Diego, California, for the 50-year interval from 1884 to 1933 inclusive, tabulated to investigate the existence of a 5-year cycle.

TABLE 1

Seasonal Rainfall at San Diego, California

Years	*1*	*2*	*3*	*4*	*5*
1884–1888........	8.7	17.0	8.3	9.8	11.0
1889–1893........	15.0	10.5	8.7	9.3	5.0
1894–1898........	11.9	6.2	11.8	5.0	5.2
1899–1903........	6.0	10.4	6.2	11.8	4.4
1904–1908........	14.3	14.7	10.6	8.5	10.2
1909–1913........	9.8	12.0	10.7	6.0	9.8
1914–1918........	14.4	12.5	10.1	8.0	8.7
1919–1923........	8.9	7.1	18.6	6.4	5.7
1924–1928........	5.8	15.7	14.7	8.7	7.1
1929–1933........	10.7	10.8	13.2	10.6	4.3
Averages ($\bar{y}_s$)...	10.55	11.69	11.29	8.41	7.14

There is an indicated increase from the first average to the second, followed by a regular decrease from the second to the last, or fifth average.

Now apply the analysis of variance method (see above, p. 231), where

$$
\begin{aligned}
m &= 5; n_s = 10; N = 50; \bar{y} = 9.816; n_1 = 5 - 1 = 4; n_2 = 50 - 5 = 45 \\
\bar{y}_s &= 10.55, 11.69, 11.29, 8.41, 7.14 \\
V_s &= \sum 10(\bar{y}_s - 9.816)^2 \div (5 - 1) = 10 \times 15.357 \div 4 = 38.4 \\
V_r &= [\sum(y-10.55)^2 + \sum(y-11.69)^2 \div \sum(y-11.29)^2 + \sum(y-8.41)^2 \\
&\quad + \sum(y - 7.14)^2] \div (50 - 5) = [100.48 + 109.13 + 112.71 + 40.70 \\
&\quad + 59.71] \div 45 = 422.73 \div 45 = 9.4 \\
Z &= \log_e \sqrt{38.4}/\sqrt{9.4} = 0.703
\end{aligned}
$$

From Fisher and Yates (1938), table V, the values of Z for the 20 %, 5 %, 1 %, and 0.1 % points are respectively 0.22, 0.48, 0.67, and 0.90. Therefore, since 0.703, the observed value of Z, is somewhat greater than 0.67, the probability is less than 0.01. The approximate extrapolated value of the probability corresponding to the median of the last three values of T in

$$
\begin{aligned}
0.84 \times 0.703 \div 0.22 &= 2.68 \\
1.65 \times 0.703 \div 0.48 &= 2.42 \\
2.33 \times 0.703 \div 0.67 &= 2.44 \\
3.10 \times 0.703 \div 0.90 &= 2.43
\end{aligned}
$$

is 0.008, according to Yule and Kendall (1937), appendix table 2, or Pearson (1930), table II, and may be regarded as small enough to establish the reality of the indicated cycle.

The second illustration pertains to sunspot numbers arranged with reference to a trial cycle of length, 11 years, excluding extremes in which the sunspot number exceeded 99. Consider the data corresponding to the early interval, 1749 to 1826 inclusive, presented in table 2.

TABLE 2

SUNSPOT NUMBERS FROM 1749 TO 1826*

Years	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*
1749–1759	81.0	83.0	48.0	48.0	31.0	12.0	10.0	10.0	32.0	48.0	54.0
1794–1804	41.0	21.0	16.0	6.0	4.0	7.0	15.0	34.0	45.0	43.0	48.0
1805–1815	42.0	28.0	10.0	8.0	3.0	0.0	1.0	5.0	12.0	14.0	35.0
1816–1826	46.0	41.0	30.0	24.0	16.0	7.0	4.0	2.0	9.0	17.0	36.0
Averages ($\bar{y}_s$)	52.5	43.2	26.0	21.5	13.5	6.5	7.5	12.7	24.5	30.5	43.2

* Exclusive of groups in which sunspot numbers exceed 99.

There is an indicated regular decrease from the first average through the sixth, followed by a regular increase to the last, or eleventh average.

Now apply the analysis of variance method, where

$$
\begin{aligned}
m &= 11;\ n_s=4;\ N=44;\ \bar{y}=25.59;\ n_1=11-1=10;\ n_2=44-11=33\\
\bar{y}_s &= 52.5, 43.2, 26.0, 21.5, 13.5, 6.5, 7.5, 12.7, 24.5, 30.5, 43.2\\
V_s &= \sum 4(\bar{y}_s - 25.59)^2 \div (11-1) = 956.32\\
V_r &= [\sum (y-52.5)^2 + \sum (y-43.2)^2 + \cdots] \div 33 = [1097.0 + 2312.76\\
&\quad + \cdots] \div 33 = 265.0\\
\sqrt{V_r} &= \sqrt{265.0} = 16.27\\
Z &= \log_e \sqrt{956.32}/\sqrt{265.0} = \log_e 1.898 = 0.6408
\end{aligned}
$$

For $n_1 = 10$ and $n_2 = 33$, the values of Z corresponding to the 20 %, 5 %, 1 %, and 0.1 % points are respectively 0.19, 0.38, 0.54, and 0.71 (Fisher and Yates, 1938, table V). Thus the probability is less than 0.01. The approximate extrapolated values of T are respectively

$$
\begin{aligned}
0.84 \times 0.6408 \div 0.19 &= 2.83\\
1.65 \times 0.6408 \div 0.38 &= 2.74\\
2.33 \times 0.6408 \div 0.54 &= 2.75\\
3.10 \times 0.6408 \div 0.71 &= 2.75
\end{aligned}
$$

and corresponding to the value, 2.75, the probability for n = infinity has the value 0.003, according to Yule and Kendall (1937), appendix table 2, or Pearson (1930), table II, which is so small that the evidence is conclusive in favor of the reality of the cycle.

In general such calculations of the probability corresponding to trial cycles of various lengths can be used as criteria in selecting the best estimate of cycle length.

Moreover, the same procedure, which was illustrated by cycle problems, can be applied to the combination of any number of sequences in which the observations in each sequence are tabulated with reference to the values of any independent variable, arranged in its order of magnitude.

Reality of a Regularity Indicated by Series of Group Averages Defining Multiple Regression

More generally, the dependent variable is a function of a number of independent variables which may be mutually correlated. The net relation of the dependent variable to any one of the independent variables considered can be presented by a series of averages of the dependent variable, corrected to constant values of the other independent variables and arranged according to increasing values of the selected independent one. For example, McEwen's method of successive approximations to group averages (McEwen and Michael, 1919; McEwen, 1920) is one way of making such a computation of multiple curvilinear regression without first assuming the forms of the functions.

An outline of the procedure for estimating the significance of the results obtained by this method follows:

M = total number of groups or columns to be averaged corresponding to all of the independent variables
N = number of values of the dependent variable
I = number of independent variables
y = any observed value of the dependent variable

$$\left.\begin{array}{c} {}_1\bar{y}_s \\ {}_2\bar{y}_s \\ \cdot \\ \cdot \\ \cdot \\ {}_I\bar{y}_s \end{array}\right\} =$$

corrected group averages of the dependent variable corresponding respectively to the 1st, 2nd, · · ·, Ith independent variable

${}_1\bar{y}$ = weighted average of values of ${}_1\bar{y}_s$
${}_2\bar{y}$ = weighted average of values of ${}_2\bar{y}_s$
· ·
· ·
· ·
${}_I\bar{y}$ = weighted average of values of ${}_I\bar{y}_s$
n_s = number of entries in column s
V_s = overall variance between columns =

$$\frac{\sum n_s({}_1\bar{y}_s - {}_1\bar{y})^2 + \sum n_s({}_2\bar{y}_s - \bar{y})^2 + \cdot \cdot \cdot + \sum n_s({}_I\bar{y}_s - {}_I\bar{y})^2}{M - I = n_1}$$

iy' = any value of y corrected to constant values of all but the ith independent variables

$$V_r = \text{residual variance} = \frac{\sum_s \sum (iy' - iy_s)^2}{N + (I - 1) - M = n_2},$$

where i denotes any one of the independent variables. The numerator is also equivalent to $\sum(y - Y)^2$, where Y equals the computed value of the dependent variable. The significance is found as before from $Z = \log_e\sqrt{V_s/V_r}$.

Among the group averages of the independent variables, one, usually a central average, is selected for each independent variable. Then the group averages of the dependent variable corresponding to those of any independent variable are corrected to the selected constant averages of the other independent variables. Thus, one average of the dependent variables of each sequence will be the same for each independent variable. Accordingly, in computing V_r, the degrees of freedom equal

$$n_2 = N - [M - (I - 1)] = N + (I - 1) - M,$$

since this constant average should be counted only once. In the more elaborate treatment where a linear regression is computed in R of the groups, the foregoing value of n_2 would have to be reduced by R, and the averages in the numerator of V_r would be replaced by the corresponding linear regression function. Also, if a linear interpolation is computed for any number of intervals between successive groups, the foregoing value of n_2 should be reduced by the number of such intervals. At the most this number would be $(M - \mathrm{I})$. Finally, if it is desired to test the significance of the net relation to the ith independent variable, the value of the variance between columns would be

$$_iV_s = \frac{\sum n_s(i\bar{y}_s - i\bar{y})^2}{_im - 1},$$

where $_im$ equals the number of columns averaged to show the net relation to the ith independent variable, and $\sum_1^I {_im} = M$.

The significance of a computed value Y can be tested with the aid of "Student's" tables (1925), or table I, (pp. 118-119) of Pearson and Wishart (1942), where $n = n_2$ equals the number of degrees of freedom. The complement of the tabular entry is the probability that the average of a sample of size $n + 1$ will differ from the population average by more than t times the standard deviation of the average of the sample. Moreover, we may regard the complement of this tabular entry as the probability that a single observation in a sample of size $n + 1$ will differ from the population average by more than t times the standard deviation of the sample. Accordingly, we may use the results of the theory of small samples in estimating the significance of the computed value Y as follows: For $t = \alpha/\sqrt{V_r}$, and $n = n_2$ in the tables, the complement of the entry equals the probability that a computed value will exceed the observed value by more than $\alpha = t\sqrt{V_r}$.

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ORGANIC PRODUCTIVITY OF AN ATOLL

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(Contribution from the Scripps Institution of Oceanography, New Series, No. 411)

Abstract--The production of organic matter by phytoplankton in the waters in and around the northern Marshall Islands is extremely low. The amount of plankton swept across the reefs of these islands by the wind-driven currents is grossly inadequate to support the animals living on the reefs. The reef community, consisting of attached algae and animals, is self-supporting; all the algae produce at least as much organic matter as all the animals consume. The rate of production of organic matter by an atoll as a whole - water, reef, and bottom - is several times as high as that of the surrounding sea, and permits maintenance of a marine population considerably denser than that of the ocean. The maximum possible rate of growth of the reef is found to be 1.4 cm per year.

Measurements of the oxygen and phosphate content of the waters in and near some of the atolls of the northern Marshall Islands yield evidence on how these coral structures remote from any terrigenous influence maintain themselves both as geographical features and as biotic communities supporting marine populations considerably denser than those of the surrounding waters. Conclusions of this kind can be drawn from such measurements because of the fact that, in the formation of organic matter, oxygen is produced and phosphate consumed, while in the biological combustion of organic matter these processes are reversed. Thus, during a time interval, the appearance of oxygen or the disappearance of phosphate in an identifiable body of water is a measure of the production of organic matter.

The recent comprehensive review by YONGE [1940] of the biology of corals makes any partial review of earlier work by the present writers unnecessary and indeed supererogatory. SHEPARD [1948, pp. 251-278] has reviewed the geology of atolls.

The standing population of plankton inside and especially outside the lagoons of the northern Marshalls is very small. The average depth at which the Secchi disc disappeared in the open sea was 41 m. According to the data of UTTERBACK [1936] see also SVERDRUP, JOHNSON and FLEMING [1942, pp. 82-84], this is representative of the clearest oceanic water and indicates a very small content of suspended matter. The average Secchi disc reading in Rongelap Lagoon was 18 m. While oceanic water is generally more transparent than this, waters as shallow as the lagoons, with an average depth of 49 m, are seldom so transparent. The conclusion that the standing population is small is supported by data on biochemical oxygen demand obtained by Donald B. Johnstone and on plankton catches obtained by Martin W. Johnson.

The rate of production of organic matter in the surface water was measured by the difference in oxygen content between bottles kept in the light and dark for eight or 24 hr. At eight stations outside Rongelap Atoll (see Table 1) the mean difference was less than 0.01 ml per liter which is equivalent to less than 0.005 mg of carbon per liter fixed as organic matter per day. The mean production of oxygen in 24 hr was 0.04 ml at eleven stations in Eniwetok Lagoon and 0.01 ml at seven stations in Rongelap Lagoon, equivalent to 0.02 and 0.005 mg of carbon respectively. In view of the large standard deviations at most stations the apparent difference in the rate of production between Eniwetok or Rongelap Lagoon and the open sea cannot be considered significant. Compared with the measured rate of production in sea water in other parts of the world all of these values are small [see RILEY 1941, p. 84, reproduced in SVERDRUP, JOHNSON and FLEMING, 1942, p. 938].

On the eastern reefs of Rongelap Atoll the ocean water, driven steadily across the reef from sea to lagoon by the trade wind waves, undergoes readily measurable changes in its oxygen and phosphate content because of the activities of the sedentary reef organisms. The presumptively productive section of a reef extends from the depth of the compensation point on the seaward slope of the reef (the sedentary animal community goes even deeper) upward through the surf zone and across the reef top to whatever point is selected as marking the inner edge of the reef, and beyond which the bottom is considered part of the lagoon. Only between the surf zone and the inner edge of the reef was the current steady enough in direction to make measurements possible.

Table 1--Oxygen production in surface ocean waters near Rongelap Atoll

Date	Location	Light condition	Oxygen content after eight-hour exposure				Average	Daily oxygen production
1946			ml/l	ml/l	ml/l	ml/l	ml/l	ml/l
June 24	Five miles NE of Kabelle Island	light	4.23	4.21	4.19	4.18	4.203	0.02
		dark	4.19	4.18	...	...	4.185	
June 24	Ten miles NE of Kabelle Island	light	4.21	4.20	4.20	...	4.203	-0.01
		dark	4.21	4.21	...	...	4.210	
June 24	Fifteen miles NE of Kabelle Island	light	4.22	4.20	4.20	...	4.207	0.00
		dark	4.22	4.20	...	...	4.210	
June 25	Two miles S of South Pass	light	4.36	4.35	4.33	...	4.347	0.03
		dark	4.30	4.30	...	...	4.315	
June 25	Two miles S of Pigan Pass	light	4.31	4.30	4.28	...	4.297	-0.06
		dark	4.37	4.35	...	...	4.360	
June 25	Two miles S of Kaeroga Pass	light	4.34	4.33	4.30	...	4.323	0.01
		dark	4.33	4.30	...	...	4.315	
July 29	Five miles E of Kabelle Island	light	4.32	...	...	...	...	0.01
		dark	4.31	...	...	...	...	
July 30	Six miles W of West Pass	light	4.36	...	...	...	...	0.07
		dark	4.29	...	...	...	...	
							Mean	0.01

For the purpose of making these measurements, four stations were selected, spaced equidistant from the surf zone across to the inner edge of the reef north of Bokujarito Island, Rongelap Atoll. The depth, velocity, and temperature were measured and oxygen and phosphate samples taken at each station approximately every three hours, tide permitting. During the period of high tide, it was impossible to work on the reef. From the data thus obtained (Table 2) the product of (a) the velocity, (b) the cross section, and (c) the difference in oxygen content between the surf zone and the inner edge of the reef can be computed and gives the total oxygen consumed or produced by the reef section between the limits of the sampling.

A second series of measurements at the same site and a series at another location on the eastern reef of Rongelap Atoll gave accordant figures.

The reef community during the night low tide consumed 0.22 ml of oxygen per sec per cm of reef measured perpendicular to the direction of the current (see Table 3), which amounts, on the average, that is, at half tide, to consuming 0.16 ml of oxygen from each liter of water flowing over the reef. This amounts to one-sixth of the oxygen removed by micro-organisms from each liter of oceanic sea water in several days or a week during the biochemical oxygen demand measurements (see Fig. 1). As the water spends only ten to 20 min in crossing the reef, it is unlikely that filtration is efficient enough to remove even ten per cent of the nutrient matter which bacteria can oxidize in a week. The plankton caught with a No. 8 net corresponds to only 0.3 per cent of the organic matter consumed by the reef. The reef organisms, therefore, can hardly be supported by the organic matter brought to them from the open sea and must be dependent on a portion of that synthesized on the reef.

From observations made at different times of day, and by using some reasonable assumptions about the rate of photosynthesis at different times of day, it is possible to construct a curve showing the rate of oxygen exchange and hence of organic matter metabolism by the reef throughout 24 hr. Integration of the curve thus obtained (see Fig. 2) indicates that during a whole day there was a small excess of oxygen production over oxygen consumption. As this excess is only about 25 per cent of the total oxygen produced during the daylight hours, its absolute value is subject to considerable uncertainty. However, it is clear that on the reef top, between the surf zone and the inner edge, the daily production of organic matter by the photosynthetic organisms at least equalled the consumption of organic matter by all the organisms. The gross daily production of organic matter by the reef top (equal to the daily apparent photosynthesis plus the concurrent respiration) was 22 liters of oxygen or 12 gm of carbon per cm perpendicular to the direction of flow of current. On the 300-m wide reef this amounts to 4.0 gm/m^2 of carbon per day.

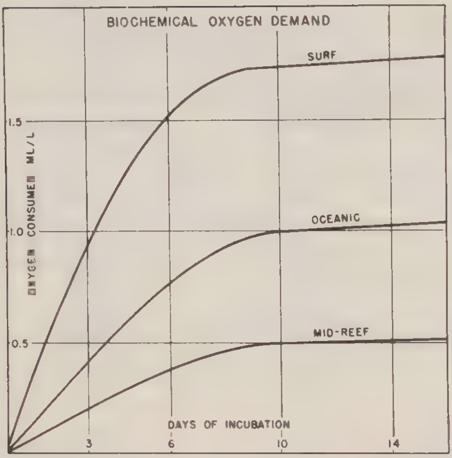

Fig. 1--Biochemical oxygen demand; data furnished by Donald B. Johnstone

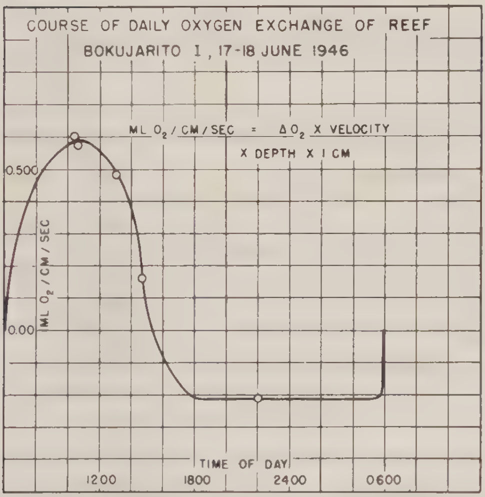

Fig. 2--Oxygen production (values above zero) and oxygen consumption (values below zero) by the reef community

The density of the population of algae, mostly nullipores, on the seaward face of the reef in and outside of the surf zone, leads to the presumption that the productivity of that area is high. The biochemical oxygen demand of ocean water and of water from the middle of the reef were both appreciably less than that of the surf zone water. As the surf breaks over the face of the reef, organic matter is washed from the reef and carried a short distance out to sea, to be again hurled against the reef with the next breaking wave. Tentatively, the conclusion may be drawn that the whole reef community from the seaward slope inward produces even more organic matter than shown by the direct measurements, which were made only on the inner portion of this community.

The data on biochemical oxygen demand (Fig. 2) are not consistent with the data on oxygen consumption by the reef (Table 3). According to the former, organic matter equivalent to more than 1.0 ml of oxygen per liter disappeared from the water between the surf zone and mid-reef. According to the latter, only 0.16 ml of oxygen was consumed from each liter of water as it crossed the reef. We are unable to explain this discrepancy to our entire satisfaction.

The higher portions of the reef, represented by the tide pools, may be considered as relatively sterile. The maximum rate of oxygen consumption in such a pool was only about 1/50 that of the densely populated areas between the islands where the circulation of water is good. The bottoms of these pools contain a few corals, many of which are dead and covered with a great number of foraminiferal tests. The rate of oxygen production during daylight hours, in the pools studied, was not sufficient to balance the consumption of oxygen during 24 hr. Orr and Moorehouse [ORR, 1933], during the course of the Great Barrier Reef Expedition, made similar diurnal studies on tide pools isolated from the oceanic circulation. In these pools the living coral were very abundant, and the changes which they observed they attributed almost entirely to these corals and their associated zooxanthellae. Their data indicate that during a 24-hr period there was a net oxygen production. The pools on the reef at Rongelap Atoll, however, are nonproductive areas.

From the data given, it is possible to obtain a crude estimate of the total organic production of Rongelap Atoll. The somewhat uncertain figure for gross oxygen production in the surface waters of the lagoon is 0.01 ml per liter per day. Because of the rapid vertical mixing and the considerable illumination at all depths, a uniform rate can be assumed throughout the $4 \times 10^{10} m^3$ of water in the lagoon. The total daily production is, therefore, of the order of 0.2×10^9 gm of carbon per day fixed as organic matter. This rate, restated as 0.2 gm/m^2 of carbon per day (over the $810 \times 10^6 m^2$ of lagoon), can be taken as close to the rate of organic production in the ocean waters surrounding the atolls. The total daily production of the atolls is larger first because of the reef community of photosynthetic organisms and second because of the bottom community. The total production of the $28 \times 10^6 m^2$ of reef can be computed as 0.1×10^9 gm of carbon per day. Data are not available for the productivity of the lagoon bottom, but the population of photosynthetic organisms is relatively sparse, and it is likely that the contribution of each square meter of the bottom is much less than that of the reef. The oxygen content of the bottom waters of the lagoon, because of the large volumes of water involved, would probably not be a sensitive indicator of bottom activity. In any case there is no measurable daily cycle in the oxygen content of the bottom waters. The total production of the atoll is, Table 2--Stations on section across reef -- Bokujarito Island, June 17-18, 1946

Date and time	Station 1 (surf zone)			Station 2	Station 3	Station 4 (inner edge)	Change in Oxygen content
	Oxygen content	Depth	Velocity	Oxygen content	Oxygen content	Oxygen content	
June 17	ml/l	cm	cm/sec	ml/l	ml/l	ml/l	ml/l
10^h20^m	4.21	18	35	4.85	5.19	...	0.98
11^h50^m	4.25	..	..	4.50	4.77	4.80	0.55
14^h40^m	4.28	64	84	4.34	4.31	4.31	0.03
17^h50^m	4.31	..	..	4.23	4.27	4.29	-0.02
22^h00^m	4.09	18	35[b]	4.03	3.94	3.74	-0.35
June 18							
01^h00^m	4.19	..	..	4.27	4.02	...	-0.17
04^h00^m	4.26[a]	..	..	...	4.25[a]	...	-0.10
10^h30^m	4.49	20	73	4.57	4.67	4.88	0.39

[a] Position approximate [b] Estimate

Table 3--Oxygen consumption and growth rate of reef at Bokujarito Island, Rongelap Atoll

Item	Description	Value
1	Oxygen content of water flowing onto reef top just inside surf zone, ml/l	4.09
2	Oxygen content of water leaving reef top on lagoon side, ml/l	3.74
3	Decrease in oxygen content of water while crossing reef, ml/l	0.35
4	Depth of water, cm	18
5	Velocity of current, cm/sec	35
6	Oxygen consumption of reef top, ml/sec/cm of reef normal to current	0.22
7	Width of reef, m	300
8	Oxygen consumption of reef top, $ml/m^2/hr$	262
9	Average rate of coral respiration, ml/gm/hr	0.0059
10	Average coral population of reef top, gm/m^2	4.4×10^4
11	Average growth rate of coral, gm new coral formed/gm coral/yr	0.76
12	Growth rate of reef, $gm/m^2/yr$	3.4×10^4
13	Average density of coral, gm/cm^3	2.5
14	Growth rate of reef, cm/yr	1.4

then, greater than the sum of the lagoon water and reef production (0.3×10^9 gm of carbon per day) but less than what would appear if the whole bottom of the lagoon were as productive as the reef ($810 \times 10^6/m^2/day = 3 \times 10^9$ gm C/day).

It can be suggested that the primary reason for the productivity of atolls relative to the surrounding waters is that on these elevated structures sedentary algae (including zooxanthellae) find a footing in the upper water zones where light intensity is sufficient for active photosynthesis. Rather than filtering organic matter, the atoll community as a whole absorbs inorganic nutrients from the passing Equatorial Current. This suggestion rests on the view that sedentary algae utilized the available supply of inorganic nutrients more effectively than a plankton population can, but is not meant to imply that the algae of atolls are more effective than those of other shores.

From measurements of the oxygen consumption by the whole reef top in the dark can be derived an estimate of the maximum possible rate of growth of the reef. This can be done by dividing the measured oxygen consumption of the reef by the average of known rates of coral respiration at the same temperature and thus arriving indirectly at an estimate of the amount of living coral on the reef. From this estimate, by means of published growth rates of coral, it is possible to compute the growth rate of the reef. The advantages of the method are first that it avoids the almost insuperable difficulties of sampling and measuring to arrive at a direct measurement of the reef population and second that it estimates coral growth from a process with which it is undoubtedly closely linked, that of coral respiration. The errors of measurement of coral respiration pointed out by YONGE [1937] do not enter here, because both our measurements and the published ones were made in the same way. The greatest error in our method lies in the assumption that the total respiration of the reef is identical with the respiration of the lime-depositing organisms. Although other types of organisms do not constitute a large part of the mass of the community, some, like bacteria, have respiratory rates many times as large as that of the corals and may account for the greater part of the oxygen consumption by the reef.

The data used are shown in Table 3. Items 1 to 8 are direct consequences of the fact that water flows steadily in one direction across the reef. The average rate of coral respiration, item 9, is based on data from YONGE, YONGE and NICHOLLS [1932, p. 218]. Data published by MAYOR [1924a, p. 19] and VERWEY [1931, pp. 175-176] as well as our own direct measurements of coral, respiration are accordant with these. The average growth rate of coral item 11, is calculated from data of MAYOR [1924b, p. 62-64]. The average density of coral (item 13) was determined by K. O. Emery.

The growth rate thus computed is believed to be larger than the actual rate, but it is of the same order of magnitude as estimates obtained by other methods and to the extent that it is independent enhances their credibility.

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THE PRODUCTION OF PHENOL AND PARA-CRESOL BY MARINE BACTERIA[1]

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The early literature contains many reports of the production of phenol and *p*-cresol by the putrefaction of proteins by mixed cultures of bacteria (Baumann, 1877; Weyl, 1878; Baumann and Brieger, 1879; Baumann, 1879; Weyl, 1879*a*,*b*). Blumenthal (1895) demonstrated the production of phenol from beef and fibrin by a pure culture of *Escherichia coli-communis* as well as by mixed cultures. Rhein (1917) and Berthelot (1917) studied the production of phenol from peptone and L-tyrosine by strains of *E. coli*. Rhein (1918) found that phenol was produced from *p*-hydroxybenzoic acid as readily as from L-tyrosine, but not from seven other possible intermediates. He postulated that *p*-hydroxybenzoic acid is an intermediate in the production of phenol from L-tyrosine, and that phenol is therefore produced by an oxidative attack on the β-carbon atom of L-tyrosine.

Sieke (1921) tested 23 species of bacteria, many of them common pathogens or commensals, for the ability to produce phenol or *p*-cresol from peptone. Only two strains of *E. coli*, *Pasteurella avicida*, and Perez's ozena bacillus responded. The methods used did not permit the author to distinguish between phenol and *p*-cresol. Rhein (1918) reported the isolation of an obligate anaerobe from soil that produced *p*-cresol in brain medium, and later (1922) published a description of the organism, *Clostridium cresologenes*. He also described a strain of *Clostridium tetanomorphum* that produced phenol in the same brain medium.

Hanke and Koessler (1924) made a study of the production of phenol by strains of *E. coli* using quantitative analytical methods. They found that certain strains produced tyramine from tyrosine in an acid medium, but produced phenol in an alkaline medium. Other strains produced no tyramine or phenol. Brief notes on the production of phenol and *p*-cresol by marine bacteria were published by Stone and Machamer (1947) and Updegraff (1947).

EXPERIMENTAL METHODS AND RESULTS

Media. Since most of the inocula were marine or estuarine sediments, cultures were prepared with media containing from 10 to 75 per cent filtered and aged sea water diluted with distilled water and containing 0.01 per cent added ferric phosphate. Suitably diluted sea water enriched with traces of iron and phosphate provide for the mineral requirements of fresh water and soil forms as well as marine microorganisms. Media were sterilized by autoclaving at 122 C for 20 minutes, after which the pH was adjusted to the desired value by the addition of sterile N/1 sodium hydroxide or hydrochloric acid. Many different media have been employed in this investigation. In order to avoid frequent repetitions of formulas, the composition of some of those most frequently employed are given in table 1.

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Methods for detection and estimation of phenol and p-cresol. For rapid routine testing of cultures for phenol and *p*-cresol the Marquis reaction, as described by Rhein (1917, 1918, 1922), was found to be the most useful method. Rhein made the test by adding a drop of 10 per cent formalin to 5 ml of culture in a test tube and pouring about 1 ml of concentrated sulfuric acid down the side of the tube. At the point of contact of the sulfuric acid with the upper aqueous layer, a violet-red ring with a ring of white turbidity above formed in the presence of phenol. In the presence of *p*-cresol or mixtures of phenol and *p*-cresol containing 10 per cent or more of *p*-cresol, a brown ring formed with a white turbidity above. The sensitivity of the reaction is about 1 part of phenol or *p*-cresol in 40,000 parts of water. In applying the Marquis reaction, it was found to be more convenient and quite as satisfactory to use a reagent containing 1 per cent formalin in concentrated sulfuric acid, thus eliminating the necessity of adding the formalin separately.

TABLE 1

List of media

MEDIUM NO.	COMPOSITION
1a	Difco peptone 5 g, $FePO_4$ 0.1 g, agar 20 g, 75% sea water 1 liter, pH 7.4 to 8.0
14a	Neopeptone 1 g, L-tyrosine (Eastman) 0.25 g, $FePO_4$ 0.1 g, 75% sea water 1 liter, pH 7.5 to 7.9
14b	Neopeptone 1 g, L-tyrosine (Eastman) 0.25 g, $FePO_4$ 0.1 g, 10% sea water 1 liter, pH 7.5 to 7.9
15a	L-Tyrosine (Eastman) 0.4 g, calcium lactate (U.S.P.) 1 g, ascorbic acid (cp) 0.2 g, 75% sea water 1 liter, pH 7.3
23a	L-Tyrosine (Eastman) 0.25 g, $FePO_4$ 0.1 g, 75% sea water 1 liter, pH 7.7 to 7.9

Although the specificity of the reaction is high enough to make it very useful, a number of interfering substances have been found in cultures. High concentrations of hydrogen sulfide inhibit the development of a color. Indole gives a violet ring, and tryptophan and peptone give a brown ring. However, these substances do not give the layer of white turbidity characteristic of phenol and *p*-cresol. No trouble was experienced with interfering substances in properly designed media. No interfering substances have been derived from microbial action on L-tyrosine. Peptone does not give rise to interfering substances if it is used in concentrations of one gram per liter or less. Even in cultures containing high concentrations of peptone or casein, all interfering substances may be removed by simple fractionation procedures involving steam distillation or solvent extraction of the culture. Other phenol reactions that have been used on such purified fractions for identification and estimation of phenol and *p*-cresol are Millon's reaction, Pauly's diazo reaction, and bromine water.

Pauly's reaction was used by Rhein (1918, 1922) for distinguishing between phenol and *p*-cresol. Phenol gives a greenish-yellow color, whereas *p*-cresol gives a red-orange tint. As little as 5 per cent of *p*-cresol in a mixture of phenol and *p*-cresol alters the color from yellow to orange. This reaction, used in conjunction with the Marquis reaction, provides a method of obtaining the approximate composition of mixtures of phenol and *p*-cresol.

The isolation of phenol and *p*-cresol was achieved by ether extraction or steam distillation of the cultures, or by procedures involving both steam distillation and ether extraction. The weakly acidic nature of phenols facilitates their separation from interfering substances.

Phenol and p-cresol production by enrichment cultures. The production of phenol or *p*-cresol proceeded rapidly in enrichment cultures inoculated with 0.1 g or more of marine mud incubated either aerobically or anaerobically. *Para*-cresol was only rarely produced in cultures incubated aerobically, although phenol was usually formed under these conditions. A strongly positive test for phenol, equivalent to a concentration of 0.01 to 0.1 per cent in the medium, was often obtained after 16 to 24 hours' incubation, either aerobically or anaerobically at 27 C. The phenol often disappeared from the enrichment cultures after several weeks' aerobic incubation, but persisted under anaerobic conditions. More than a score of cultures, grown in 50 to 75 per cent sea water medium containing from 0.02 to 0.2 per cent tyrosine, from 0.5 to 10 per cent peptone, and 2 per cent casein were tested qualitatively for phenol and *p*-cresol, and 13 cultures were analyzed quantitatively for these products by a steam distillation procedure followed by application of the method of Aleksevski and Tarasova (1935) as cited by Snell and Snell (1937).

All the cultures grown on L-tyrosine medium containing no other organic substrate produced phenol but no cresol. Those grown anaerobically on peptone or casein produced only *p*-cresol. Yields of phenol from a medium containing 0.2 per cent L-tyrosine were from 52 to 58 per cent of the theoretical on the basis of a theoretical yield of 1 mole of phenol per mole of L-tyrosine. Yields of *p*-cresol from 2 per cent casein and peptone medium were from 42 to 86 per cent of the theoretical yield from the tyrosine content of the substrates.

Qualitative tests for tyrosine and tyramine in the residual culture solution after removal of the ether-soluble fraction were negative. The fate of the tyrosine not converted to phenol or *p*-cresol in these cultures remains unknown.

Distribution of phenol- and p-cresol-producing bacteria. Preliminary results showed that medium 14a (table 1) gave excellent results for routine examination of marine materials for phenol-producing bacteria, whereas 14b was suitable for soil and fresh water inocula. These media contain sufficient peptone to promote rapid growth of phenol-producing bacteria, but not enough to interfere with the application of the Marquis test for phenol and *p*-cresol. By adding known concentrations of phenol to the sterile medium and comparing the Marquis reactions with those of the cultures, the phenol concentration could be estimated within 20 per cent.

The medium was tubed at 5 to 10 ml per tube, and 0.1 to 1.0 g of inoculum was added to each tube of sterile medium. Cultures were incubated 2 to 4 days, either aerobically or anaerobically in a McIntosh and Fildes jar under hydrogen, at 28 C. A 2-ml portion was removed and tested for phenol and *p*-cresol with Marquis' reagent. If hydrogen sulfide was recognized by its odor, the 2-ml portion was acidified with a few drops of 2 normal sulfuric acid, and a current of air was drawn through it for a few minutes to remove the hydrogen sulfide before applying the Marquis reaction. Cultures showing negative Marquis reactions were incubated another 3 to 7 days and tested again before being discarded.

A total of 155 samples, all from southern California unless otherwise indicated, distributed as follows, were used for inocula:

(1) 58 one-tenth-gram surface samples of marine sediments from the intertidal zone to 10 miles offshore from southern California and Louisiana; (2) 47 samples of marine sediments from 0.5 to 4 feet below the surface of the sediment from southern California waters, the Bering Strait, and the Antarctic Continental Shelf; (3) 30 samples of sediment cores down to 381 feet below the surface of the Louisiana tidelands; (4) 7 one-gram samples of sea water; (5) 1 one-tenth-gram sample of sea weed (*Zostera*); (6) 1 mussel (*Mytilus*); (7) 4 barnacles; (8) 3 one-gram samples of oil sump pit water; (9) 1 sample of oil well cellar water; (10) 3 samples of garden soil.

The results, given in the percentage of the samples that produced phenol in the described test, are presented for each type of inoculum: (1) 90, (2) 19, (3) 0, (4) 57, (5) 100, (6) 0, (7) 0, (8) 0, (9) 100, (10) 33.

A brief survey of the distribution of bacteria producing *p*-cresol was made on 0.1- to 0.5-g portions of 27 of the surface marine sediment samples and the sample of oil well cellar water. Three sediment samples and the oil well cellar water, tested in a medium composed of 2 per cent neopeptone in 50 per cent sea water, gave 100 per cent positive tests for *p*-cresol-producing bacteria. The other tests, performed in medium 14b (table 1) gave 67 per cent positive tests.

The principal facts learned from this survey are as follows: (1) Phenol- and *p*-cresol-producing bacteria are widely distributed in marine and brackish water sediments from the intertidal zone and from areas up to 10 miles offshore. The finding of such organisms in most of the 0.1-g samples examined indicates that there are ordinarily more than 10 of them per gram of moist sediment. (2) The texture of the sediment does not seem to be a determining factor, as the organisms are abundant in sand and in fine mud. (3) Phenol-producing bacteria may be found in numbers from 1 to 10 per gram in very shallow water, where they may be stirred up from the bottom by turbulence, but are not found in appreciable numbers in water far from shore. (4) Like most other marine bacteria, the numbers of phenol-producing bacteria appear to decline with depth in the sediment. (5) Bacteria capable of producing phenol and *p*-cresol do not appear to be found in association with marine animals such as mussels or barnacles. (6) Phenol-producing bacteria may be found in soil and oil well cellar water.

Isolation of pure cultures of phenol-producing bacteria. The isolation of pure cultures of phenol-producing bacteria proved to be a difficult task. No pure cultures of *p*-cresol-producing bacteria were obtained. It was found that initial failures to isolate pure cultures of phenol producing bacteria were due to the fact that the organisms soon lost the ability to produce phenol when grown on the surface of agar plates. Several different plating media were used, including nutrient sea water agar, medium 14a with the addition of 2 per cent agar, and a sea water agar in which L-tyrosine was the sole organic addition other than agar. The pH was adjusted to 7.4 to 7.8. Many phenol-producing enrichment cultures were streaked and plated on such media. Isolations were also attempted in deep agar shake cultures. More than 100 colonies were picked and transplanted into medium 14a before a pure culture was obtained which produced phenol. The colony from which it was picked did not differ in appearance from any of the other colonies on the plate, and the morphology of the organism was identical. This culture was plated out again on tyrosine sea water agar, and two identical colonies were picked and transferred to medium 14a. One produced phenol and the other did not, although the morphological and cultural characteristics of the two strains appeared identical. The phenol-producing culture was plated out a third time on tyrosine sea water agar. All of seven colonies picked and transferred to medium 14a produced phenol.

Using the same methods, a total of 11 pure cultures of phenol producing bacteria were isolated. Ten of these were isolated from marine sediments, and one from oil well cellar water. The characteristics of these cultures were studied by the methods recommended in the *Manual of Methods for the Pure Culture Study of Bacteria* (1945, 1946) as well as by the special methods to be described. The organisms are facultative anaerobes, but aerobic conditions were used in the classification tests in order to make the results comparable with published studies on similar bacteria. All media were prepared with 75 per cent aged sea water.

It is believed that the similarities warrant including all of these cultures in a single species. They are closely related to *Achromobacter harveyi*, described by Johnson and Shunk (1936) and now listed under the name *Pseudomonas harveyi* by Breed *et al.* (1948). They differ from this species in that they are not luminescent and that most strains of the phenol-producing bacterium ferment glycerol whereas *Pseudomonas harveyi* does not. Johnson and Shunk made no mention of the action of their organism on tyrosine. In view of these differences, the phenol-producing organism is believed to constitute a new species. A full description of the organism, and a comparison with *Pseudomonas harveyi*, the only species of *Pseudomonas* which appears to resemble the phenol-producing organism closely, will be published elsewhere.

Characteristics of Pseudomonas sp.

Morphology: All cultures were gram-negative rods 0.8 to 1.5 by 1.5 to 5 μ, occurring singly, in pairs, and sometimes in short chains, with rounded ends.

The rods were sometimes slightly curved, and the ends were occasionally somewhat pointed. All cultures were motile. The flagellation of 7 cultures was studied, and all were found to possess a single polar flagellum.

Cultural characteristics: several types have been recognized on nutrient sea water agar: (1) flat, iridescent, circular, smooth colonies with somewhat undulant borders, spreading rapidly to a size of 5 to 10 cm in diameter in 24 to 48 hours at 28 C; (2) circular, entire, smooth, convex, white translucent colonies 0.1 to 1 mm in diameter after 1 to 3 days at 28 C; and (3) colonies identical to type 2 except about one-fourth the size. At temperatures of 37 C or above type 1 colonies are never formed. All three types of colony may occur on a single plate made from a single pure culture of a type 1 strain. Type 2 cultures may give rise to type 3 colonies also, but type 3 cultures produce only this colony type. After 2 to 3 weeks' incubation at 28 C, type 2 colonies grew to 5 to 9 mm in diameter, and the edges sometimes became striated. Type 3 colonies seldom exceeded 0.5 mm in diameter, even on prolonged incubation. Pigment was not formed on 0.5 per cent peptone agar, but, in agar fortified with 0.02 per cent of L-tyrosine, the colonies became brown, and a brown pigment diffused throughout the medium. In sea water gelatin plates, liquefaction was ordinarily so rapid that colony form could not be observed. On sea water agar slants, the spreading types gave abundant, viscous, spreading, grayish, iridescent growth. Other types gave less abundant echinulate to beaded growth without iridescence. In nutrient sea water broth, all cultures gave rapid growth with abundant uniform turbidity, a thin pellicle or ring, and a viscid sediment. In fresh water nutrient broth, all 7 strains tested failed to grow.

Nitrates were reduced to nitrites by all cultures. Indole was produced by all cultures (tested by Gore's and Ehrlich's methods). Hydrogen sulfide production from peptone was variable under aerobic conditions, but always positive when the organisms were grown anaerobically in a synthetic medium containing several amino acids fortified with 0.1 per cent L-cystine. The ZoBell-Feltham (1934) method was used for the detection of hydrogen sulfide. Starch was rapidly hydrolyzed to reducing sugars and finally converted to acids by all strains except one. Ammonia was produced from peptone by all strains. Casein was hydrolyzed rapidly by all strains except one.

Fermentations: The most active strains fermented 16 carbohydrates out of 22 tested with the production of acid but no gas. The least active strain fermented only 8 carbohydrates. Glucose, mannose, fructose, and maltose were fermented by all strains. Gas was never produced. A modification of the micromethod of Devignat (1944) using nutrient sea water broth containing 2 per cent of the carbohydrate and bromcresol purple indicator was used.

Oxygen tension: All cultures were facultative anaerobes. Anaerobic growth was tested in medium 14a containing sufficient hydrogen sulfide to reduce the Eh to −6 mv. Phenol was produced in nearly theoretical yields (0.7 to 1 mole of phenol per mole of L-tyrosine in the medium) under either aerobic or anaerobic conditions, although aerobic cultures occasionally failed to produce phenol, forming melanine by a typical tyrosine-tyrosinase reaction instead. Variants that produce melanine instead of phenol could not be induced again to produce phenol, but were otherwise identical with the parent strain.

Effect of pH: Seven cultures were tested for growth and phenol production in medium 28 (L-tyrosine 0.4 g, calcium lactate 1 g, $FePO_4$ 0.1 g, 75 per cent sea water 1 liter) under aerobic conditions at pH values varying from 3.4 to 8.4. Growth was vigorous from pH 7.0 to 8.4, and phenol was produced in most cases. No growth or phenol production was noted from pH 3.4 to 4.3. The same seven cultures were also tested for growth and phenol production under anaerobic conditions in a McIntosh-Fildes hydrogen jar in medium 33 containing 0.25 per cent peptone and 0.025 per cent L-tyrosine and heavily buffered with potassium phosphate. The pH varied from 5.2 to 10.0. Growth was obtained from pH 6.4 to 10.0, although it was feeble at the upper limit. Phenol was produced from pH 6.4 to 9.0 in all cases, and in all but two cultures at pH 9.6. The growth of the bacteria modified the pH in spite of heavy buffering, reducing it to pH 8.9 to 9.1 in cultures originally at pH 9.6. The final concentration of phenol did not depend on pH, as it reached 75 per cent or more of the theoretical yield whenever it was produced.

Temperature requirements: The temperature requirements of the same seven strains were determined on nutrient yeast extract sea water agar plates at temperatures ranging from 3 to 47 C. Optimum growth was obtained at 30 to 40 C. Only one culture grew at 47 C, and only one at 3 C. Good growth was obtained at 19 and 27 C. Of 3 cultures tested under anaerobic conditions in 2 per cent peptone sea water broth, all grew vigorously at 43 C and two grew less strongly at 47 C.

Nutrient requirements: All cultures grew well and produced phenol under aerobic conditions in medium 23a (table 1), a sea water medium containing L-tyrosine as the sole organic addition. The same result was obtained with a synthetic medium prepared with distilled water, cp salts, and L-tyrosine. The ability of 6 strains to utilize 10 simple carbon compounds as sole nutrients was also tested in a synthetic medium prepared with cp salts and distilled water with 0.1 per cent of the carbon compound to be tested. Glutamic acid and asparagine supported excellent growth of all strains under aerobic conditions, and fair anaerobic growth. Lactic and acetic acids were fairly good carbon sources. Glycine and cysteine supported good growth of some but not all strains. Formic acid, pyruvic acid, cystine, and methionine failed to support growth. These experiments demonstrate that the organism is able to utilize very simple carbon compounds as sources of energy, and is able to synthesize all growth factors required in its metabolism.

Mechanism of phenol production: Rhein (1918) found that phenol was produced from *p*-hydroxybenzoic acid as readily as from L-tyrosine by *E. coli*, and postulated that *p*-hydroxybenzoic acid was therefore an intermediate in the reaction. In order to determine whether the same mechanism is followed by *Pseudomonas* sp., a medium identical to 14a (table 1) was prepared in which the L-tyrosine was replaced by *p*-hydroxybenzoic acid. Each strain was inoculated into a tube of this medium, and at the same time into a tube of medium 14a.

All cultures were incubated aerobically at 28 C, and tested after 24 hours and again after several days for phenol. Growth was equally vigorous in both media. Phenol was always produced in medium 14a, but never in the *p*-hydroxybenzoic acid medium.

It may be concluded that *p*-hydroxybenzoic acid is not an intermediate in the production of phenol by *Pseudomonas* sp. Unfortunately, no other possible intermediates were available for testing. Attempts to follow the production of phenol by washed cell suspensions failed to yield useful data. Active suspensions could only be obtained by growing the cells anaerobically and washing the cells as rapidly as possible. Such cell suspensions produced phenol only under anaerobic conditions. The mechanism of phenol production by this organism therefore remains unknown.

Hydrogenase activity: Washed cell suspensions of three cultures grown anaerobically and one culture grown aerobically were tested for hydrogenase by the methylene blue reduction method of Stephenson and Stickland. The cells grown anaerobically contained an active hydrogenase capable of transferring hydrogen to methylene blue, but the cells grown aerobically had no hydrogenase activity. Hydrogenase therefore resembles the enzyme system that produces phenol in that it is produced only under anaerobic conditions.

Investigations of the ability of other species of marine bacteria to produce phenol and p-cresol from L-*tyrosine.* The observation that all the pure cultures of phenol-producing bacteria isolated belong to the same species makes it seem likely that the ability to perform this reaction is not widely distributed among different species of marine bacteria. In order to investigate this question, 5 pure cultures of sulfate-reducing bacteria, isolated from marine sediments by Dr. W. D. Rosenfeld, and 62 pure cultures of aerobic or facultative marine bacteria from the collection described by ZoBell and Upham (1944) were tested for their ability to produce phenol and *p*-cresol from L-tyrosine. The sulfate-reducing bacteria (*Desulfovibrio aestuarii*) were cultivated anaerobically in 60-ml glass-stoppered bottles in medium 15a. The other 62 cultures were incubated aerobically in tubes of medium 14a. All these cultures were maintained at 27 to 28 C until good growth was obtained, and were then tested for phenol and *p*-cresol with Marquis' reagent. In no case was a positive test obtained. It may be concluded that the ability to produce phenol is rare among different species of marine bacteria.

DISCUSSION

An inconsistency will be noted in that cultures "incubated aerobically" usually produce phenol, whereas it is stated that the enzyme system that forms phenol is produced only under anaerobic conditions. A possible explanation is that cultures incubated aerobically in cotton-plugged tubes rapidly utilize all dissolved oxygen in the medium and become anaerobic beneath the surface, thus permitting the phenol-producing variant to develop. This interpretation is supported by the observation that many cultures incubated aerobically in liquid media permanently lose the ability to produce phenol, but such cultures incubated anaerobically do not lose this ability.

Pseudomonas sp. is actively proteolytic and saccharolytic. It has very simple nutrient requirements and tolerates wide variations in Eh, pH, temperature, and composition of the medium. Its biochemical versatility and wide distribution fit it for an important role in the nitrogen and carbon cycles in marine sediments.

SUMMARY

Bacteria capable of producing phenol and *p*-cresol were found to be widely distributed in marine sediments from the continental shelf of southern California and from the intertidal zone of Louisiana.

Studies of enrichment cultures showed that bacteria were present that rapidly produced phenol or *p*-cresol in sea water media containing L-tyrosine, casein, or peptone. Phenol was usually produced in media containing free L-tyrosine and little or no peptone, but *p*-cresol was usually produced in media containing only peptone or casein incubated under anaerobic conditions.

Attempts to isolate pure cultures of *p*-cresol-producing bacteria were unsuccessful, but 10 pure cultures of phenol-producing bacteria were isolated from marine sediment samples and 1 from oil well cellar water.

This organism, believed to be a new species of *Pseudomonas*, is a facultative anaerobe that produces phenol from L-tyrosine, peptone, and casein. When it is cultivated under aerobic conditions, variants arise that have permanently lost the ability to produce phenol from L-tyrosine, but instead produce melanine by a typical tyrosine-tyrosinase reaction.

The mechanism of phenol production is unknown. It differs from that of *Escherichia coli* as *p*-hydroxybenzoic acid is not an intermediate.

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ZOOPLANKTON AS AN INDEX OF WATER EXCHANGE BETWEEN BIKINI LAGOON AND THE OPEN SEA

Martin W. Johnson

(Contribution from the Scripps Institution of Oceanography, New Series, No. 413)

Abstract--The zooplankton (small floating animals) are useful indicators of water currents in the area where they live. Of the holoplanktonic (permanently planktonic) forms found in Bikini Lagoon, 90 per cent or more occur also in the surrounding open sea. The lagoon plankton, however, is characterized by (1) a number of endemic species not found outside the lagoon except where washed out by outflowing currents, and (2) a concentration within the lagoon of many forms that occur normally also in the outside surface waters. Both of these features are dependent upon the degree of dispersal of the plankton and are therefore directly correlated with the semiclosed circulation which the lagoon imposes upon the water that flows in over the eastern and northeastern reefs.

A study of the vertical distribution and diurnal vertical migration of the endemic copepod Undinula vulgaris, and of the general plankton, reveals that much of the lagoon plankton lives mainly in the deeper slowly (0.1 knot) eastward-moving counter current which as a water mass represents 70 to 90 per cent of the living space in the lagoon. Even during the night when much of the plankton migrates towards the surface into the faster (0.3 knot) westward-moving water, about two-thirds of the plankton still remains within the deeper counter current.

Much of the oceanic plankton swept into the lagoon thrives there and becomes concentrated so that the average concentration per cubic meter of water of the eleven most common animal groups is about four times higher than in the outside north-eastern area, and twice higher than the outside western-southern area of principal outflow. The increased concentration found in the outside water to the west and south indicates an outwash from the lagoon in that area and is shown especially by such forms as Undinula vulgaris and Tretomphalus planus (foraminifer), which occur abundantly in the lagoon, but were not found in the area immediately to the east and north of the atoll.

The restricted water flow within the lagoon is biologically important in conserving also the transitory planktonic larval stages of lagoon and reef fishes and bottom-living animals.

The presence of Copilia mirabilis (copepod) mainly in the southern half of the lagoon and outside around the southern and south-eastern periphery of the atoll suggests a slow flow of southern water into the lagoon between Enyu and Bikini Islands and through the eastern part of Enyu Channel.

By the term plankton is meant all of the organisms, usually microscopic or semi-microscopic that float about in the sea with little or no resistance to water currents. Thus, in general, they are dispersed and transported in a manner dependent upon the prevailing current system. The animal plankton consists not only of such forms as are permanently planktonic all of their lives (holoplanktonic), but also of the transitory young or larval stages of bottom-living forms, such as crabs, certain shrimp, clams, and others, and of the fishes.

In most planktonic studies it is customary to apply the results of hydrographic surveys as an aid to explaining the biology of an area. The mechanism presented by the current system is a factor of prime importance in production, concentration, and dispersal of the planktonic life. This dependence upon currents, therefore, sometimes makes it possible to take the converse point of view in order to gain information and corroborative evidence on the nature of water currents through a study of the plankton. The countless myriads of floating forms are in a sense tiny drift bottles, which, if recognized as to kind and source, are useful indicators. Similarly the concentration of a population presupposes a certain type of circulation that minimizes dispersal.

Perhaps 90 per cent or more of the holoplanktonic forms found in Bikini Lagoon occur also in the outside surrounding water. The lagoon plankton fauna are, however, characterized by two strik-

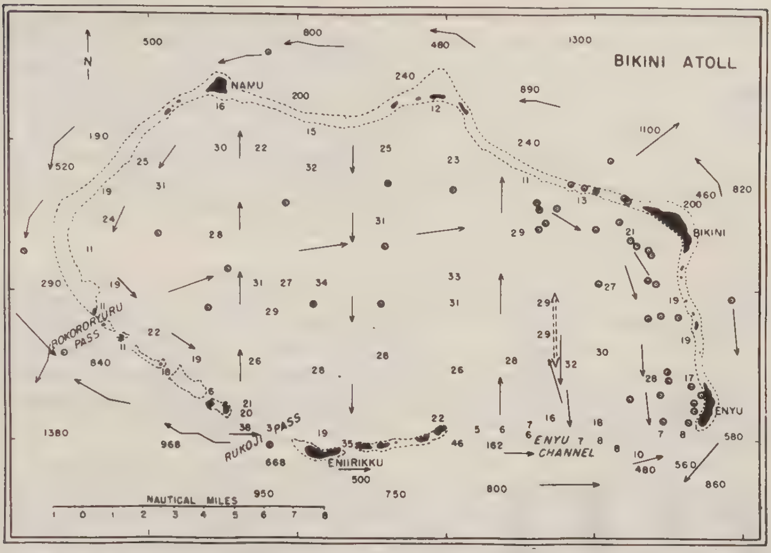


Fig. 1--Positions of plankton hauls taken at Bikini Atoll March 10 to May 18, 1946; the arrows indicate course of horizontal hauls; the circles indicate vertical hauls; the figures are depths in fathoms

ing features: (1) A number of the important species are endemic to the lagoon and are seldom or never found outside except at localities where they have been washed out of the lagoon over the reef or through passages. (2) There is a concentration of many forms that also occur normally in the outside surface water. In general the plankton concentration in the Marshall Island area is relatively very sparse.

The capacity of the lagoon to foster an endemic fauna, and the ability of the Lagoon to concentrate the fauna common to the Lagoon and the outside water, result largely from the same mechanism. This mechanism is inherent in the current pattern which results mainly from the retarding effect that the lagoon has on the oceanic water which it intercepts from the North Equatorial Current.

Bikini Atoll is a coral-capped volcanic mountain which rises abruptly from the ocean floor at a depth of over 2000 fathoms. The Lagoon has a maximum depth of about 35 fathoms [EMERY, TRACEY, and LADD, 1949]. At low tide it is completely isolated from the sea except for a number of passages forming gaps of six to 35 fathom in depth in the reef along the southern and southwestern periphery (see Fig. 1).

Methods--The plankton samples forming the basis for this report were collected with Clarke-Bumpus plankton samplers, which give a measure of the volume of water filtered through the net. The nets used with these samplers for the regular series of hauls were of No. 2 bolting silk. In this series 64 samples are from inside the lagoon and 54 outside the lagoon.

Inside the lagoon, two samplers were usually towed 20 to 30 minutes sumultaneously at one- and ten-fathom depths. Deeper horizontal towing within the lagoon was inadvisable because of the many coral heads or pinnacles rising from the bottom. For the 24-hour series in the lagoon three samplers were towed at 1-, 10-, and 25-fathom depths over a course that had previously been carefully surveyed to determine that no coral obstructions would be encountered. Outside the lagoon, the samplers were towed simultaneously at 1-, 10-, and 40-fathom depths. The positions and courses over which the samples were taken are shown in Figure 1.

The regular hauls were checked qualitatively by many irregular qualitative samples collected with larger nets towed at various places inside and outside the lagoon at depths up to 260 fathoms.

This report deals mainly with observations made between March 10 and May 18, 1946, before the atomic bomb blasts. Samples taken after the blasts (not shown in Fig. 1) were concerned principally with conditions within the lagoon. The few samples taken outside as late as August 8, 1946, and contrasted with the spring samples, showed no appreciable change in concentration in the plankton.

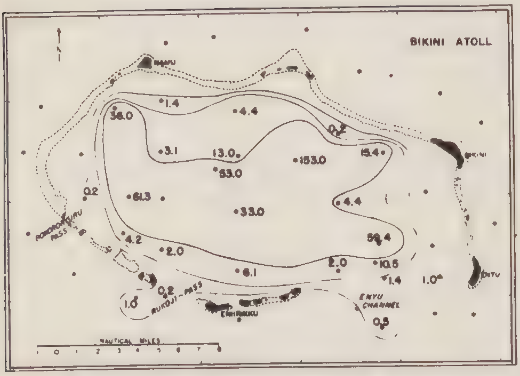


Fig. 2--Undinula vulgaris, number per cubic meter of water by stations (black dots)

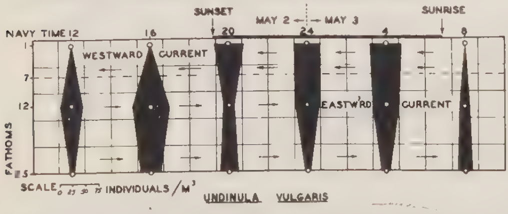


Fig. 3--Diurnal migration of Undinula vulgaris; thirty-five-minute horizontal hauls taken at surface, ten, and 25 fathoms at four-hour intervals over course shown by double dashed arrow in Figure 1

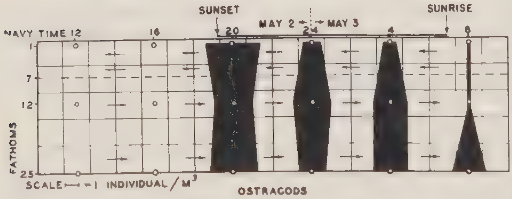


Fig. 4--Diurnal migration of Ostracods

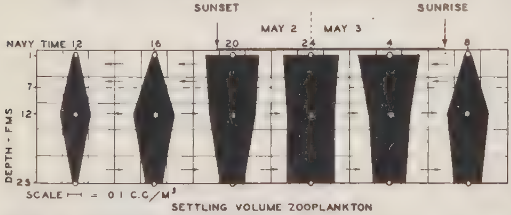


Fig. 5--Diurnal migration of total zooplankton as represented by settling volume

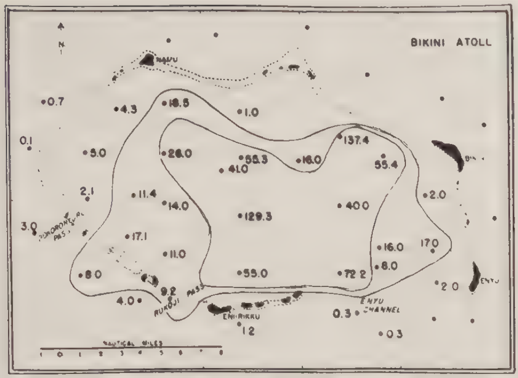
Currents indicated by maintenance of endemic species--In some areas such as the Gulf of Maine, for example, the endemic population is correlated with a large circular flow of water which produces a semi-closed system. In Bikini Lagoon the current mechanism is much smaller and operates mainly in a vertical rather than horizontal plane. Its significance in Bikini is the retarding effect it has on the water passing through the lagoon.

Surface water in the lagoon is driven by the prevailing trade winds in a WSW direction, whereas the water at intermediate and greater depths flows in the opposite direction as a counter current. This gives rise to sinking in the western portion of the lagoon and to upwelling against the eastern reefs [VON ARX, 1948].

In the search for endemic species in Bikini Lagoon, the most useful thus far considered are Undinula vulgaris (Dana), a copepod crustacean, and Tretomphalus planus Cushman, a pelagic foraminiferan. The latter was identified by J. A. Cushman who described the species originally from Samoa, and states that it occurs also at Fiji Islands. Both occur also in the lagoons of Eniwetok, Rongelap, and Rongerik.

Undinula vulgaris is a widely-distributed species and though reported from the open ocean it appears to be preponderantly a lagoon form in this area. Large (two millimeters) and easily recognized, it occurs in varying numbers throughout most of the Lagoon. During the period March 10 to May 18 it was present at about 90 per cent of the lagoon stations. The largest numbers (up to 255 per cubic meter of water) have been taken near the center of the lagoon (see Fig. 2). In the daytime the animals seek the deeper water strata, ten or more fathoms deep. Very few specimens were caught in the net towed at or above the one-fathom depth except at night. More will be said about this later. It is obvious that to maintain an endemic population of an amimal with a relatively long life history like that of Undinula vulgaris, and in such numerical concentrations, there must be a pattern of currents which leads to a relatively closed system with very slow flushing of at least a large part of the Lagoon. This would require the presence of a sizable counter current or some other effective retarding system. The hydrographic study has indicated that a deep slowly moving counter current exists. Thus the biological and hydrographic observations support each other on this point.

During the time that the animals are in the upper surface layer near the outwash of the Lagoon, they are in danger of being swept out through passages or over the reef. Therefore, (a) reproduction in the deeper layer would have to be at a rate sufficient to replenish the loss of numbers washed away by the surface layer, or (b) in case of slow reproduction the bulk of the population would have to spend the greater part of the time in the deep slowly-moving counter current. That the latter occurs in Bikini Lagoon is indicated by a study of the diurnal vertical migratory journeys of Undinula vulgaris and a number of other planktonic forms (see Fig. 3, 4, and 5). From these figures it will be seen that not only Undinula but the bulk of the other planktonic forms avoid the more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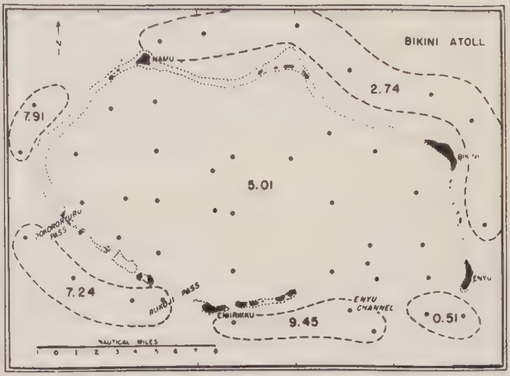
NAMU
0.7
4.3
18.5
1.0
0.1
5.0
26.0
55.3
41.0
16.0
137.4
55.4
2.1
11.4
14.0
129.3
40.0
2.0
3.0
ROKORONYURU PASS
17.1
11.0
16.0
17.0
8.0
55.0
72.2
8.0
9.2
4.0
RUKOJI PASS
ENIIRIKKU
12
0.3
ENYU CHANNEL
0.3
2.0
ENYU
BIKINI
NAUTICAL MILES
1 0 1 2 3 4 5 6 7 8

Fig. 6--Tretomphalus planus, number per cubic meter of surface water by stations (black dots)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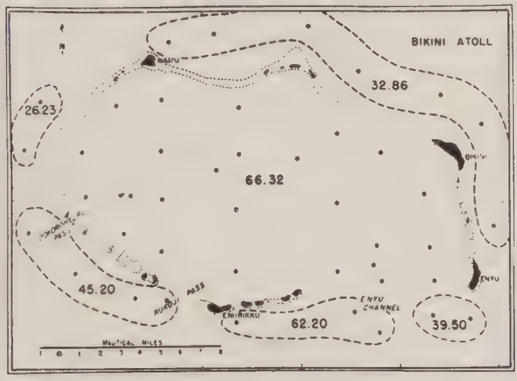
RUKOJI PASS
ENIIRIKKU
ENYU CHANNEL
9.45
0.51
NAUTICAL MILES
1 0 1 2 3 4 5 6 7 8

Fig. 7--Globigerina, average number per cubic meter of water by areas; black dots indicate stations averaged in each area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RUKOJI PASS
ENIIRIKKU
ENYU CHANNEL
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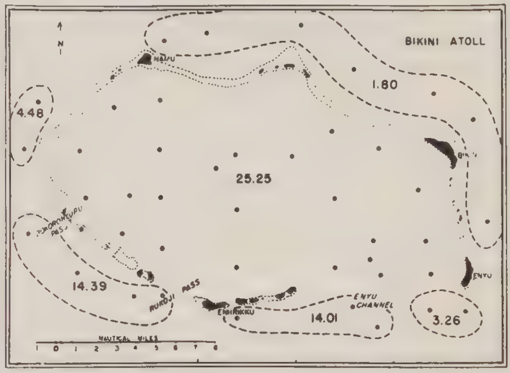
39.50
NAUTICAL MILES
1 0 1 2 3 4 5 6 7 8

Fig. 8--Copepods, average number per cubic meter of water by areas; black dots indicate stations averaged in each area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ROKORONYURU PASS
ENYU
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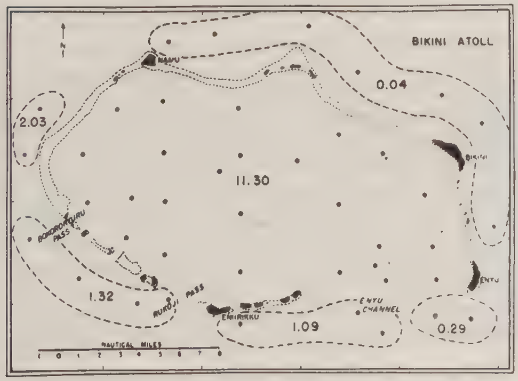
RUKOJI PASS
ENIIRIKKU
ENYU CHANNEL
14.01
3.26
NAUTICAL MILES
1 0 1 2 3 4 5 6 7 8

Fig. 9--Appendicularia, average number per cubic meter of water by areas; black dots indicate stations averaged in each area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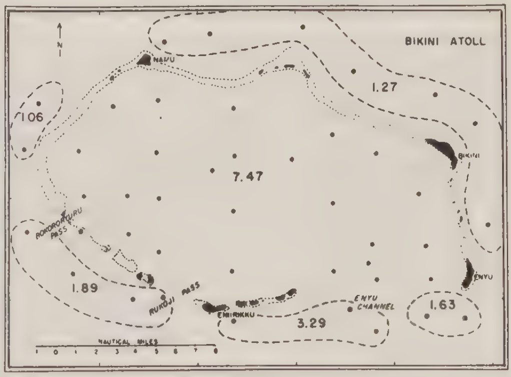
BIKINI
11.30
ROKORONYURU PASS
ENYU
1.32
RUKOJI PASS
ENIIRIKKU
ENYU CHANNEL
1.09
0.29
NAUTICAL MILES
1 0 1 2 3 4 5 6 7 8

Fig. 10--Pteropod, Creseis sp., average number per cubic meter of water by areas; black dots indicate stations averaged in each area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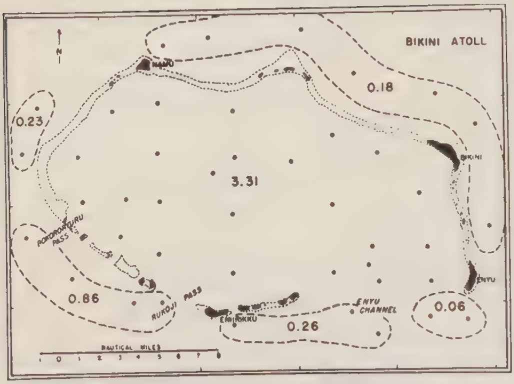
RUKOJI PASS
ENIIRIKKU
ENYU CHANNEL
3.29
1.63
NAUTICAL MILES
1 0 1 2 3 4 5 6 7 8

Fig. 11--Arrow worms, Sagitta spp., average number per cubic meter of water by areas; black dots indicate stations averaged in each area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NAMU
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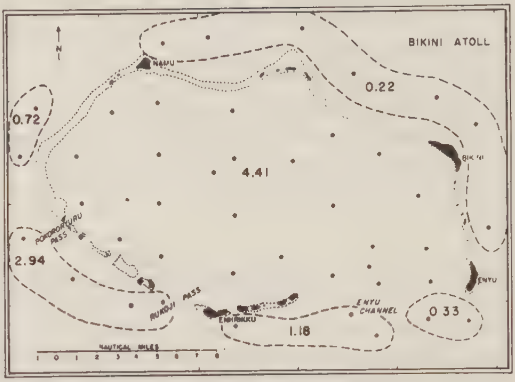
0.23
3.31
BIKINI
PORORORUTURU PASS
0.86
RUKOJI PASS
ENIIRIKKU
ENYU CHANNEL
ENYU
0.26
0.06
NAUTICAL MILES
1 0 1 2 3 4 5 6 7 8

Fig. 12--Crab larvae, average number per cubic meter of water by areas; black dots indicate stations averaged in each area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NAMU
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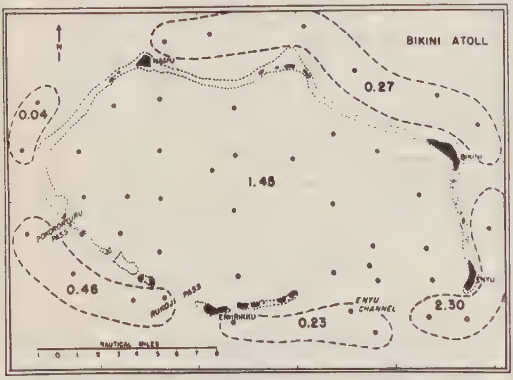
0.72
4.41
BIKINI
PORORORUTURU PASS
2.94
RUKOJI PASS
ENIIRIKKU
ENYU CHANNEL
ENYU
1.18
0.33
NAUTICAL MILES
1 0 1 2 3 4 5 6 7 8

Fig. 13--Shrimp larvae, average number per cubic meter of water by areas; black dots indicate stations averaged in each area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BIKINI
PORORORUTURU PASS
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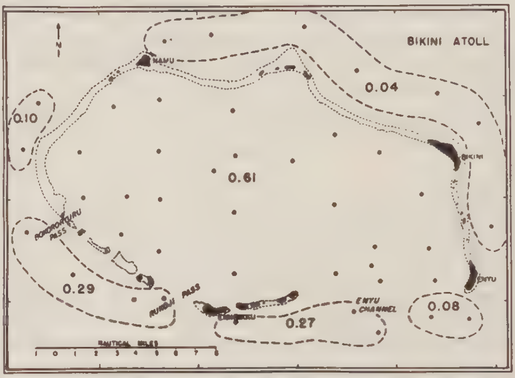
RUKOJI PASS
ENIIRIKKU
ENYU CHANNEL
ENYU
0.23
2.30
NAUTICAL MILES
1 0 1 2 3 4 5 6 7 8

Fig. 14--Fish eggs, average number per cubic meter of water by areas; black dots indicate stations averaged in each area


N
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BIKINI
PORORORUTURU PASS
0.29
RUKOJI PASS
ENIIRIKKU
ENYU CHANNEL
ENYU
0.27
0.08
NAUTICAL MILES
1 0 1 2 3 4 5 6 7 8

Fig. 15--Fish larvae, average number per cubic meter of water by areas; black dots indicate stations averaged in each area

lighted surface waters during the day and even at night a goodly portion (two-thirds or more) of the population remains in the slowly moving (average 0.1 knot) counter current. This current involves 70 to 90 per cent of the water mass of the Lagoon; in other words 70 to 90 per cent of the living space. Nevertheless, at night much of the population must be transported towards the western and southern margins of the Lagoon by the relatively fast-moving (average 0.3 knot) surface current. Depending upon wind velocity the depth of this current varies from 2.5 to 10 fathoms, with an average of 6.5 fathoms (the maximum depth of the Lagoon is about 33 fathoms). At the approach of dawn a downward movement of the animals occurs and a slow journey eastward begins. In this manner about one-third of the distance lost during the night is recovered during the day. It is probable that this is the order of events with respect to many larval forms of bottom-living adults in the lagoon and also with the oceanic forms swept into the lagoon over the eastern reefs. Biologically this is very important in conserving not only the holoplankton, but also the transitory larvae that eventually settle to the bottom of the lagoon or on the reefs to re-stock the bottom-living animals.

Tretomphalus planus was found in all parts of the lagoon, sometimes in numbers up to 175 or more individuals per cubic meter of water. The average was, however, only about 25 per cubic meter. It was present throughout the whole period of investigation (March 10 to Aug. 8) and occurred at all depths within the lagoon. The greatest concentrations were in the upper ten fathoms except in a few instances where numbers were greater in the deeper strata.

The plankton samples collected outside the lagoon yielded this species only at the stations situated along the western and southern periphery of the atoll. The greatest outside concentrations were found near the passages, thus suggesting the main route of outwash for the species as indicated in Figure 6. Apparently small numbers are also washed out over the long shallow reef extending from Bokorōryūru Pass to Namu Island. This is in keeping with the animal's habit of floating near the immediate surface. The deeper-living lagoon animals such as Undinula vulgaris are discharged through the passages (depths varying from six to 35 fathoms) rather than over the reef.

From the above observations it appears that Tretomphalus is endemic to the Lagoon, perhaps requiring shallow water during the early stages of its life history before the float chamber has been developed. This would explain its absence or scarcity in deep water outside the lagoon except where washed out on the down-current side by the prevailing flow through the lagoon. It should be pointed out here that this relationship suggests the use of Tretomphalus as an index of past oceanographic conditions of the atoll. Provided its tests are well preserved as fossils in the sediments, it should serve to show the general direction of currents that have swept through the Lagoon in past history, for though the animal is kept suspended by the float chamber while alive, there must be a gradual precipitation of defunct tests to the bottom along the course of the outflowing water.

Maintenance and concentration of oceanic plankton in the Lagoon--The salinity and temperature of the water within the lagoon differs but little from that outside. The highest lagoon salinity (34.85 $^{0}/_{00}$) is only about 0.1 $^{0}/_{00}$ higher than in the open ocean while the temperature change from about 27.02 to 27.10° C is negligible. The vertical gradients of these factors are also insignificant. In these respects the lagoon water is essentially oceanic and would therefore not be seriously inimical to most of the surface oceanic plankton coming in over the reef.

The concentration of oceanic plankton that has drifted into the Lagoon is a further indication of a semi-closed circulatory pattern in the Lagoon. Presumably this circulation would operate in a mechanical manner similar to its effect on the maintenance of the endemic fauna. In the following section it will be shown that certain forms that are common to the inside and outside may be as much as 27 times more numerous per unit of water inside the lagoon. This increased concentration doubtless results in part from better food conditions inside as a result of local production, but the reduction of dispersal must be very important.

The presence in the Lagoon of many egg-bearing specimens and a large proportion of larval and juvenile stages of species common to the outside is evidence of successful reproduction inside. In the absence of wide and uninterrupted dispersal, such as occurs outside, a concentration from both reproduction inside and recruitment from outside should occur.

In summarizing the average concentration by areas of the eleven most common animal groups, it appears that the ratios of concentration per cubic meter for (a) the outside eastern-northern area, (b) the inside lagoon area, and (c) the outside western-southern area of principal outflow, are roughly a:b:c: = 1:4:2.

Inflow and discharge of water from the Lagoon as indicated by the drift of planktonic life--When we compare the number of specific organisms occurring per cubic meter of water at stations occupied inside the lagoon with the number found in the surrounding water just outside the reefs and passages, it is seen that the concentration is almost invariably smallest in the waters outside the eastern and northern reefs. It is nearly always largest by far at the stations within the Lagoon, and intermediate at stations just outside the western and southern passages and reefs. The largest outside catches occur near Rukoji Pass and the western portion of Enyu Channel (Figs. 2, and 6 to 15). Figures 2 and 6 are especially useful since they deal with two endemic species and show clearly the route by which the species are washed out of the Lagoon. According to hydrographic studies the outflow is through these passages and over these reefs, and this is clearly corroborated by the biological evidence. The biological evidence does, however, indicate a somewhat broader outwash from Enyu Channel in the early part of the survey than the hydrographic charts indicate.

From the hydrographic survey we learn that in the open sea off Bikini there is a small north-south gradient in temperature and salinity so that the water entering the lagoon from the north is about 0.1 $^{0}/_{00}$ C colder and 0.3 $^{0}/_{00}$ more saline than that which enters the southern passes.

The plankton has not yet been studied in sufficient detail to know the extent of its usefulness in indicating other than the general routes of entry into the lagoon. The distribution of one copepod species, Copilia mirabilis, does, however, suggest that its center of distribution may be in the southern water with which it enters the lagoon through Enyu Channel and over the reef between

Bikini and Enyu Island. Forty-four per cent of the stations in the southern half of the lagoon yielded this species, but only 11 per cent in the northern half. Outside the lagoon from near Bikini Island around the southern periphery of the atoll to near Arriikan Pass on the west side, 75 per cent of the stations yielded the species. None was taken at outside stations north of these points. Nowhere was the species found in abundance.

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VON ARX, W. S., The circulation systems of Bikini and Rongelap Lagoons, Trans. Amer. Geophys. Union, v. 29, pp. 861-870, 1948.

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Relation of Plankton to Hydrographic Conditions in Sweetwater Lake

By Martin W. Johnson

A paper presented on Oct. 28, 1948, at the California Section Meeting, Riverside, Calif., by Martin W. Johnson, Assoc. Prof. of Marine Biology, Scripps Institution of Oceanography, Univ. of California, La Jolla, Calif.*

THE biology of Southern California lakes is practically an untouched field, although the physical aspects have received some attention, and were the subject in 1941 of a hydrographic report by McEwen (1). In that report the temperature cycle and related changes in the hydrogen ion distribution were considered, and the need for extensive research, including the investigation of the biological phenomena of local lakes was stressed. One of these lakes—Sweetwater—was the subject of a special investigation from June 1944 to June 1945 by members of the University of California Div. of War Research. In this investigation the diurnal and seasonal thermal structure was studied and certain aspects of the biology were included for June, July, August and November.

Sweetwater Lake is a narrow artificial body of water produced as a result of damming the Sweetwater River. About 2 miles long, it runs in a general east-west direction and is located approximately 10 miles inland, where it is exposed to the sea breezes so important to its dynamics.

Hydrography

Part of the hydrographic results of the University of California study were presented by Holtsmark and Gould (2). In Fig. 1, taken from that report, is shown the annual variation from morning to afternoon in the average depth to the top of the thermocline. From this it is seen that a considerable rise may occur daily during the summer and autumn months even though a strong stratification has developed due to a marked temperature gradient (as much as 6°–8° F. per foot) in the thermocline. These diurnal movements of the thermocline are associated with the type of alternating water circulation that has been induced by winds which in summer blow alternately from east to west and west to east. The surface currents of the lake have been measured, and from these and the temperature structure the summer subsurface currents have been deduced, as shown in Fig. 2 redrawn from La Fond (3).

During the summer there is a freshening of westerly winds in late morning. These increase during early afternoon and finally become calm about sundown. The marked thermal stratification which has developed through surface heating resists effective deep circulation and results in the well known summer stagnation common to many deep lakes. In Sweetwater Lake this stagnation reaches a maximum during August and in 1944 was confined to depths below approximately 20 ft. According to computations by McEwen (1), a wind of 30 mph. or more would be required to supply sufficient force to overturn completely or mix the waters during the period from May to October. In contrast, however, a good circulation is maintained in the epilimnion which lies above the thermocline. This is shown by the temperature structure, the well oxygenated condition of the water and the shifting of plankton populations as indicated by collections at the fixed station where observations were made.

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* Scripps Institution of Oceanography, New Series No. 414.

It is instructive to consider how the floating life of the lake is affected by these physical conditions and to see how the biological, physical and chemical studies are mutually useful in providing an integrated picture of the orderly dynamics involved in the lake environment.

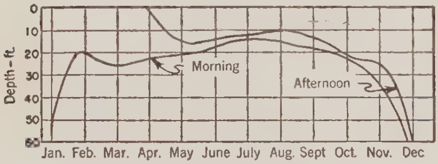

FIG. 1. Average Depth to Top of Thermocline

Biological Observations

The plankton collections and the accompanying temperature, turbidity and oxygen observations were made at a barge anchored in the deep water a short distance from the dam. Samples of plankton were collected at frequent depth intervals from the surface to near the bottom. The collections were more closely spaced near the thermocline, since the greatest populations were always found there and the lower limits of stratification of the population were most pronounced. An electrically driven pump which delivered 100 l. of water in four minutes was used for collecting the plankton. In order to confine the water intake to a stratum as narrow as possible, two 1-ft. lengths of ¾-in. pipe were connected with a tee, which in turn was attached to the lower end of a 50-ft. garden hose. The water delivered by the pump was filtered through a plankton net of No. 25 silk bolting cloth having mesh apertures of 0.064 mm. Temperatures were taken with a bathythermograph, water samples for oxygen determinations were collected with a Nansen hydrographic bottle and turbidity measurements were made with a photometer giving readings in units of microvolts. The larger the meter reading, the greater is the illumination on the photocell, and consequently a greater transparency is indicated. No absolute values can be assigned to the numbers, but they are comparable for any one set of observations on turbidity and are corrected for solar radiation.

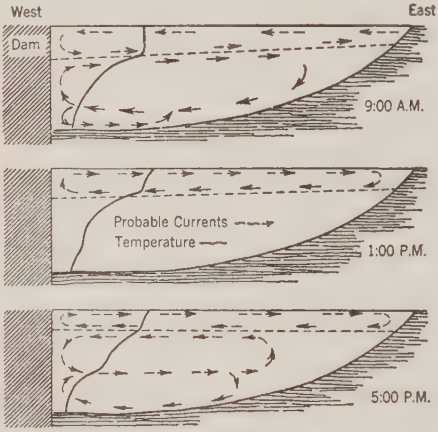

FIG. 2. Probable Currents and Temperature Structure

June 20 observations. The earliest biological observations were made in June. At this time two well defined thermoclines were present at 12 and 32 ft., respectively. The diatom *Fragilaria* was essentially the only photosynthetic organism in the plankton and had its maximum numbers between the two thermoclines (Fig. 3). Copepods, mites, and cladocera were most abundant from 20 to 30 ft. Rotifers were present mainly in and above the upper thermocline and were numerically the most abundant organisms caught.

increase in turbidity just above and within the upper thermocline. Below this level there was a gradual increase in this factor corresponding roughly to an increase in plankton volume. The most turbid water, however, was found at 33 ft., just within the lower thermocline, from which no plankton sample was available. The most transparent water occurred at 39 ft., a depth which lies in the bottom layer with uniform temperature.

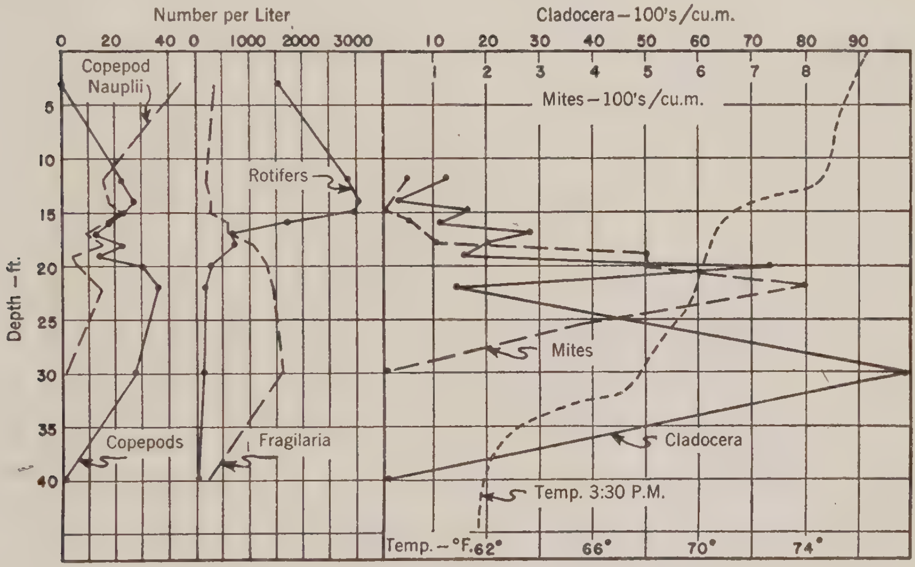

FIG. 3. Vertical Distribution of Plankton and Temperature (June 20)

The total plankton volume was small, but vertically there was a slight increase in the region of the thermocline and a second larger increase between the two thermoclines (Fig. 4). It is significant to note that in June the decline in the major population occurred at depths greater than 30 ft., indicating that living conditions at this time were tolerable at depths from 10 to 15 ft. greater than a month later (Fig. 5–8).

From the turbidity measurements it can be seen that there was a small

July 20 observations. The thermocline fluctuated at a depth near 20 ft. On this date *Fragilaria* was still important among the plants, but *Ceratium* was the dominant form (Fig. 5). *Staurastrum, Pediastrum* and *Cosmarium* were common. All of the plants showed a strong maximum just above or within the thermocline. The zooplankton, shown in Fig. 6 and 7, was strongly stratified with several maxima between depths of 12 and 22 ft. Above 12 ft. only a meager population was found, and below 24 ft. the water was

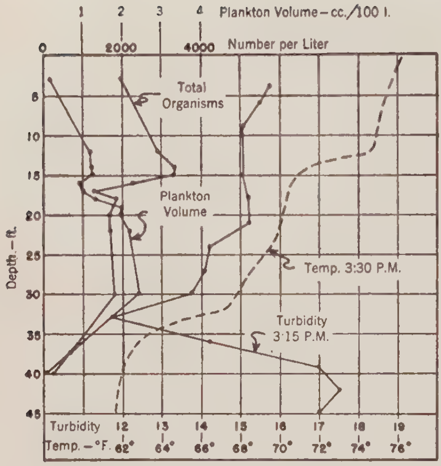

FIG. 4. Total Plankton, Turibidity and Temperature (June 20)

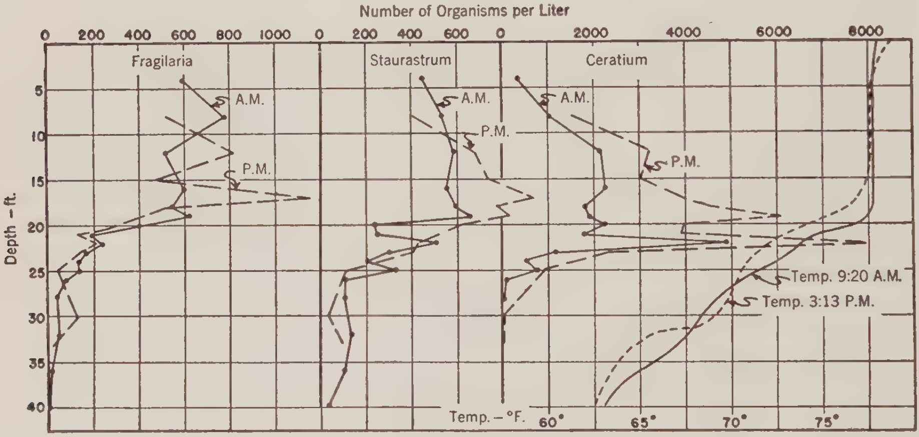

FIG. 5. Phytoplankton and Temperature (July 20)

almost completely sterile of animal life. In Fig. 8 the volume of total plankton indicates a close correlation with the transparency of the water at various depths. Compared with the June observations, however, the greatest turbidity was now at 23 ft., a rise of 10 ft. during the past month.

August 28 observations. The series of observations on this date are of greater interest in that the period of maximum stratification and stability appears to have been reached. The thermocline was between 22 and 26 ft., depending upon the time of day. *Ceratium* was still the principal unicellular photosynthetic organism but reached a maximum of only 4,200 per liter (Fig. 9). The blue-green alga, *Anabaena,* was common from 6 to 19 ft., and *Oscillatoria,* from 32 to 45 ft. Copepods and rotifers were the principal animals (Fig. 10 and 11). As in the July observations, the plankton was confined almost entirely to the water above the thermocline; below 24 ft. little other than *Oscillatoria,* and empty tests of *Ceratium* and rotifers, were noted.

The oxygen profile for this date showed a well aerated mixed layer above the thermocline with a small maximum at 20 ft., apparently resulting from the photosynthetic activity of *Ceratium* at or near that depth. Below 20 ft. there was a marked drop in the oxygen, which reached zero in the stratum from 45 ft. to the bottom.

Turbidity varied greatly, with a maximum at or just below the maximum population densities, but with a thick stratum of relatively turbid water well below the population density.

The cause of this condition is not evident from an examination of the samples collected, but it may be associated with *Oscillatoria,* which was common from 32 to 45 ft., or with an accumulation of very finely divided detrital material resulting from bacterial breakdown of the plankton above and with fecal detritus from the zooplankton. This fine detrital material might readily pass through the net, thus leaving little evidence of its existence. It will be noted also in Fig. 8 that turbid water had a tendency to occur slightly below the corresponding plankton strata.

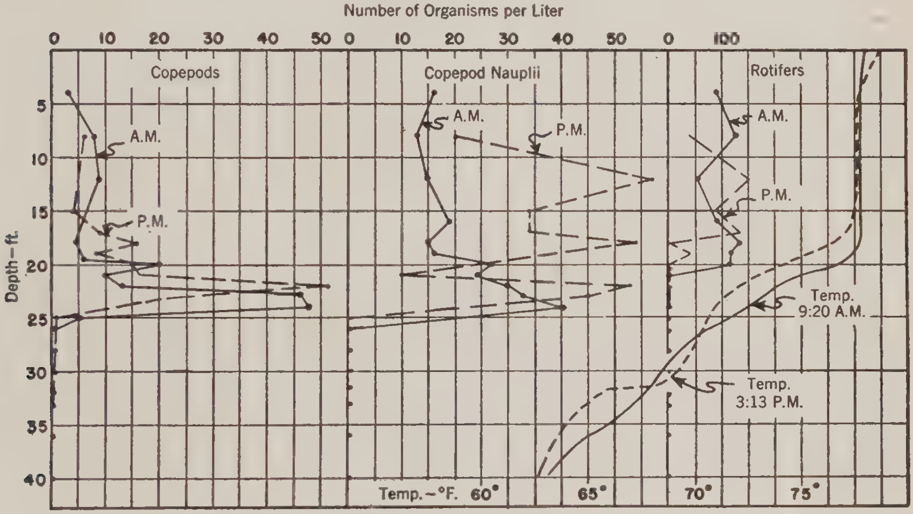

FIG. 6. Zooplankton and Temperature (July 20)

November 20 observations. A complete autumnal overturn had occurred before this date, as witnessed by uniform temperature from top to bottom, nearly uniform oxygen, transparency and a series of alternating strata of plankton from the surface to the bottom (Fig. 12). The principal phytoplankton consisted of a diatom of undetermined genus, together with *Stephanodiscus, Pediastrum,* a very few *Fragilaria* and *Ceratium.* Copepods were the most important of the larger animals and tintinnids were relatively abundant. The total plankton volume was, however, very small.

Discussion

The unpleasant tastes and odors that sometimes occur in drinking water are often associated with concentrations of certain types of microscopic floating life. It is of considerable practical interest, therefore, to learn the biology of the organisms involved and to know their relation to the hydrographic and chemical conditions of the lake. Doubtless each lake presents special problems which are in reality only variations from a general biological and hydrographic cycle common to lakes in this latitude.

The vertical position and fluctuations in the heaviest concentration of planktonic life must be items of considerable importance in determining the level from which water should be drawn from a reservoir for domestic use. The studies on Sweetwater Lake indicate that, as far as the plankton

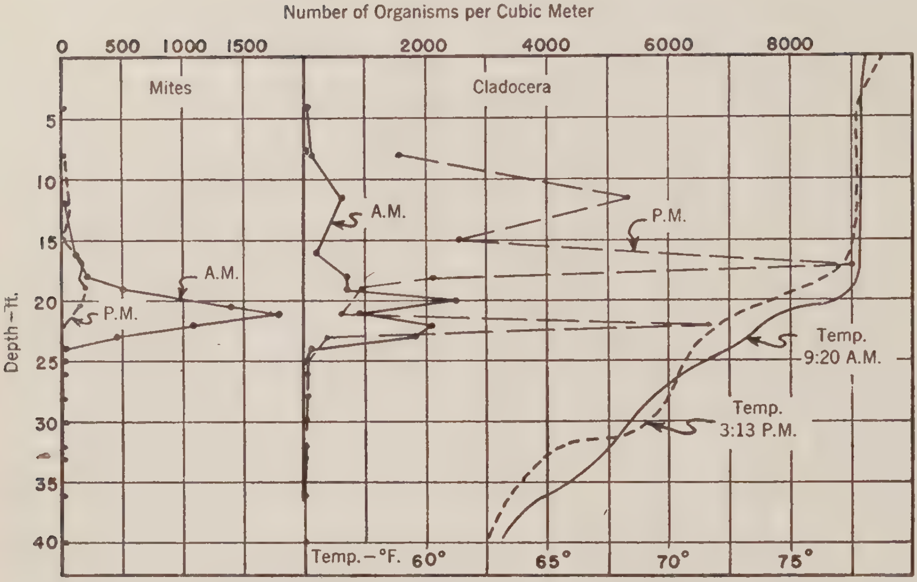

FIG. 7. Zooplankton and Temperature (July 27)

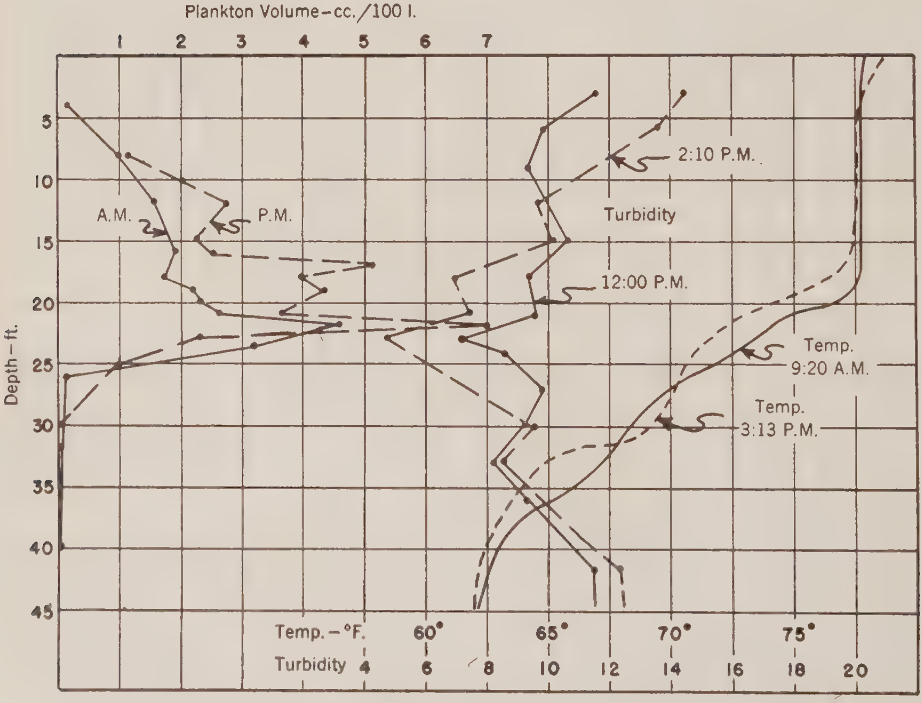

FIG. 8. Total Plankton, Turbidity and Temperature (July 20)

distribution of that lake was concerned during the summer of 1944, the best level from which to draw water would be relatively near the surface, and for depths of 10 to 25 ft. the clearest water would be obtained in the morning.

The observations for July and August are of special interest in showing how the maximum depth and abundance of the plankton at the sampling station situated just above the dam—and, therefore, near the intake—are correlated with the diurnal shift in depth of the thermocline and the direction of flow of the water.

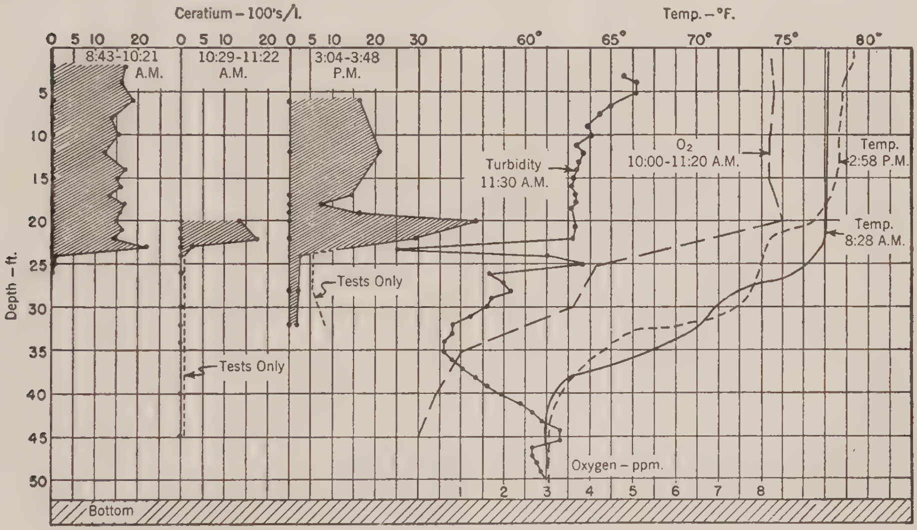

Fig. 9. *Ceratium,* Turbidity, Oxygen and Temperature (Aug. 28)

In July the vertical shift is especially clear for the copepods, rotifers and mites (Fig. 6 and 7). The upward shift of these animals is approximately 2 ft., which corresponds with the upward shift of the top of the thermocline between 9:20 A.M. and 3:13 P.M. There was also an afternoon increase in numbers of most organisms, and turbidity was likewise somewhat greater in the afternoon.

The progressive upward shift of the plankton population with the advance of the day is especially well marked in the August 28 observations. On this day the rise was approximately 4 to 5 ft. and agrees with the observed rise in the thermocline during the period. The change in population density, especially of the copepod nauplii (Fig. 10), and of *Ceratium* (Fig. 9) during the seven-hour period on August 28 is further evidence that a lateral shift of population had also occurred.

These diurnal fluctuations in plankton concentration appear to be indicative of a diurnal reversal in the direction of flow of the surface water and of a compensatory flow in the subsurface water at the thermocline, as already deduced from the hydrographic study. We have seen that the organisms reach a maximum concentration at subsurface depths, there being relatively few near the surface. During periods of easterly winds this plankton-poor water flows westward toward the dam, where it is diverted downward, replacing the plankton-rich water which now flows eastward with its population along the thermocline. When the water currents are reversed, following an increase of westerly winds during the day (*see* Fig. 2), the plankton-rich water again flows into the area near the dam. Thus, the morning samples are relatively poor in plankton compared to those collected at the same station in the afternoon. The complicating effects of vertical diurnal migration of certain animals were not studied.

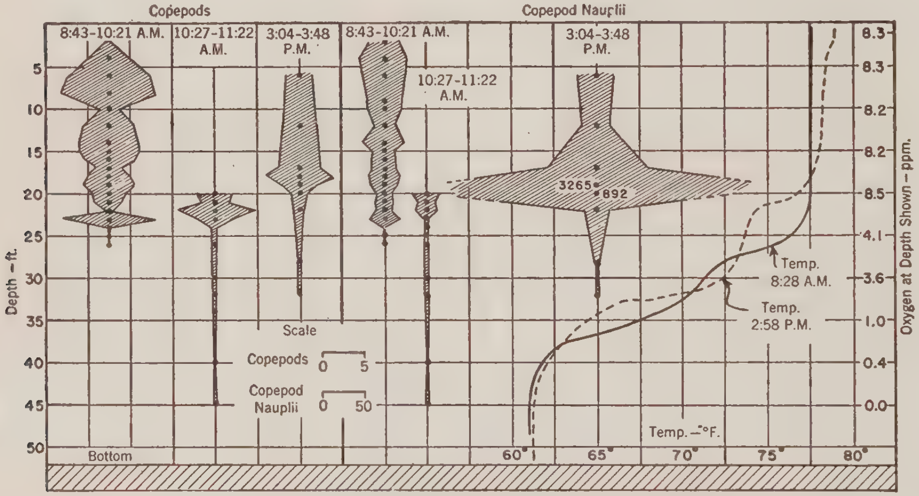

FIG. 10. Copepods, Temperature and Oxygen (Aug. 28)

The autumnal overturn is an event of prime importance to the biology of Sweetwater Lake, as in other similar lakes. During the summer period of strong thermal stratification there is a continual consumption of the mineral plant nutrients (nitrates and phosphates) by floating plants in the upper water layers. Gradually these nutrients are bound as organic substance in the bodies of the plants, or of animals feeding upon the plants, and hence must be largely precipitated into the deeper water as dead bodies or fecal detritus. On the bottom the organic material is again reduced to the mineral state through bacterial action. Because of the lack of deep circulation at this time, the oxygen of the deep water becomes more or less exhausted, carbon dioxide increases and hydrogen sulfide may develop. The nutrients regenerated at the bottom remain unused by the plants, either because of toxic substances or lack of sufficient light at that depth. Initially the lack of light is probably the cause, though the compensation depth (the depth where the oxygen production by photosynthesis and the oxygen consumption by respiration of the plants is equal) has not been determined for this lake at any season. Despite this withdrawal of nutrients from the surface to the bottom, there may still be a notable production of organic material in the surface waters.

In a report on the phosphorus cycle in a lake, Hutchinson and Bowen (4) have reviewed literature showing that there may be a series of flares of phytoplankton growth without a reduction of the phosphate content in the surface waters, or on occasions the phosphate and plankton might increase simultaneously, even in stratified lakes. Hence, it is believed that the low phosphorus concentrations in surface waters during the summer should be regarded as a steady condition which represents a more or less balanced state between phosphorus replenishment and its consumption by plants. Since there is a constant withdrawal of phosphorus, in the form of sinking particulate material, into the temporary summer storehouse below the thermocline, a question arises as to the origin of this slow summer replenishment of nutrients above the thermocline.

In an attempt to follow the cycle directly, Hutchinson and Bowen (4) used the radioactive isotope of phosphorus P^{32}. They liberated a quantity of radiophosphorus along sections across a small lake and after a week's time made tests which indicated a downward movement of 57 per cent of the phosphorus into and below the thermocline, where it was apparently out of circulation with the surface layer. The total phosphorus in the layer above the thermocline had, however, increased during the week, and it was believed that this increase was due to horizontal transport from the shallower portion of the lake with depths above the thermocline. Regenerated nutrients might therefore constantly become available from the muds in such areas, which amounted to 24.6 per cent of the lake bottom in the lake studied.

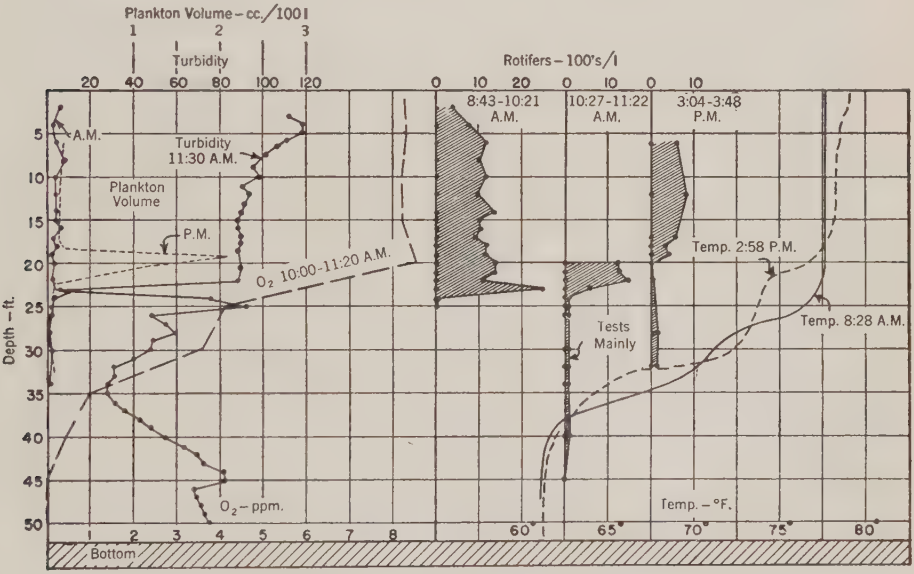

Fig. 11. Total Plankton and Rotifers (Aug. 28)

A recent review (5) of the literature dealing with the bacterial regeneration of plant nutrients presents considerable evidence that phosphates and ammonia nitrogen are rapidly liberated from diatom and copepod plankton. In lakes, doubtless, some regeneration of nutrients takes place in the free water above the thermocline, since it is known that a large bacterial population commonly exists together with the main plankton population (6). Moreover, it has been shown by several workers that the nitrogen assimilated by some plants, including diatoms, may be obtained from ammonia (NH_3) or, to some extent, even from the amino acids. Thus, it is not necessary to go through the slower formation of nitrite (NO_2) or nitrate (NO_3) before the nitrogen becomes available to the phytoplankton. This process would supplement the nitrogen that must also be liberated together with the phosphorus from muds in the littoral area.

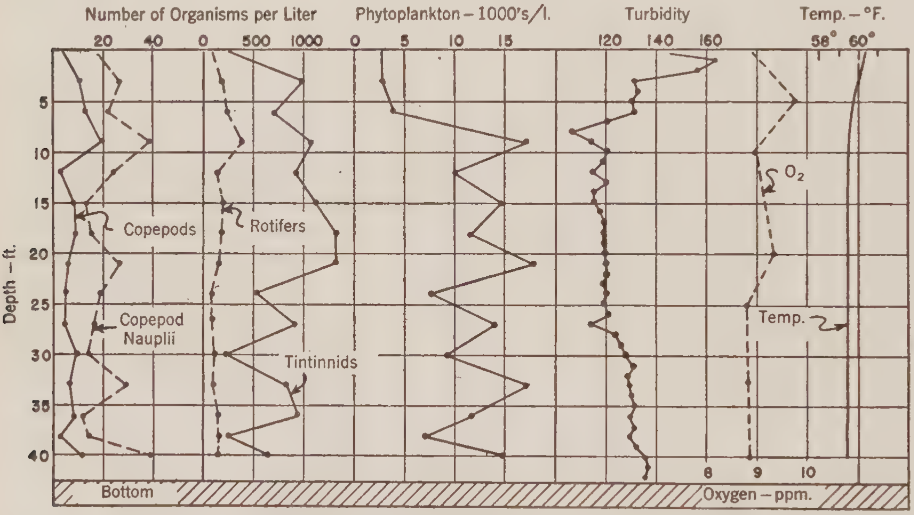

FIG. 12. Uniform Conditions Resulting From Lake "Overturn"

Acknowledgment

Most of the work forming the basis of this report was done while the author was a member of the staff of the University of California Div. of War Research at the U.S. Navy Radio and Sound Laboratory (now the U.S. Navy Electronics Laboratory), San Diego, Calif. Various members of the Oceanographic Section assisted in the study. J. H. Martin, in charge of the calibration barge at the lake, assisted especially with the turbidity measurements.

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THE BLACK BASSES (*MICROPTERUS*) OF FLORIDA, WITH DESCRIPTION OF A NEW SPECIES[1]

BY REEVE M. BAILEY AND CARL L. HUBBS

In OUR revision of the black basses we were unable, because of the paucity of critical material, to arrive at a thorough understanding of the taxonomy and distribution of the forms of *Micropterus* in certain peripheral areas, namely from Texas in the Southwest and from parts of Alabama, Georgia, and all of Florida in the Southeast (Hubbs and Bailey, 1940: 7, 15, 21, 28, Maps 1–2). Since then the accumulation of additional specimens has permitted clarification of the problem of the subspecies of spotted bass (*Micropterus punctulatus*) in Texas. All material from the rivers of eastern Texas has been identified as *Micropterus punctulatus punctulatus* and a distinct subspecies, *M. p. treculii,* has been recognized in the Colorado, Guadalupe, and San Antonio river systems (Hubbs and Bailey, 1942).

New material from the Southeast makes possible a considerable expansion of our knowledge of the systematics of the genus *Micropterus.* In this paper we (1) describe, as a distinct new species, *Micropterus notius,* the Suwannee bass, from

[1] Contributions from the Museum of Zoology of the University of Michigan and the Scripps Institution of Oceanography (New Ser., No. 415).

Ichtucknee Springs, Columbia County, northern Florida; (2) report the occurrence in Florida of the spotted bass, *Micropterus punctulatus* (regarding *M. p.: henshalli* × *punctulatus* as indigenous and *M. p. punctulatus* as presumably introduced); (3) describe and discuss, but do not name, a single large bass from the Chipola River at Marianna, western Florida; (4) discuss the long-debated status of the northern smallmouth bass, *Micropterus dolomieu dolomieu,* as an inhabitant of Florida waters, and conclude that this species has not become established there and that the "smallmouths" of reputed record size were largemouth bass; (5) treat the classification and scientific name of the largemouth bass, regarding *Huro* as 1 of the 2 subgenera of *Micropterus;* and (6) recognize the giant largemouth bass of peninsular Florida as a distinct subspecies, *Micropterus salmoides floridanus* (LeSueur), outline its intergradation with the widespread northern form, *M. s. salmoides* (Lacépède), and treat it as one element in the endemic fish fauna of peninsular Florida.

The bulk of the material on which this report is based is in the Museum of Zoology, but most of the largemouth bass from South Carolina were loaned to us by E. B. Chamberlain and E. Milby Burton from the collections of the Charleston Museum. To them we are grateful. We wish to thank Theodore H. Hubbell for suggestions and for reading the manuscript. We are indebted, also, to E. Ross Allen, Archie F. Carr, Jr., and William M. McLane, who collected many of the specimens here reported.

I

SUWANNEE BASS

Micropterus notius, new species

(Pl. I)

With the exceptions of the spotted bass and Chipola bass discussed below, the only specimens of the subgenus *Micropterus* examined by us from Florida are 6 from Ichtucknee Springs, tributary to Santa Fe River, in the limestone sink area of northern Florida. They represent a strikingly distinct species. This is believed to be a small species since our largest example, an adult male late in its fourth summer of life, measures only 218.5 mm. in standard length and 269 mm. (10.6 inches) in total length.

Since *M. notius* has scales on the interradial membranes toward the bases of the anal and soft dorsal fins, a shallowly emarginate dorsal fin, and simple pyloric caeca, it is clearly referable to the subgenus *Micropterus,* rather than to *Huro. M. notius* is to be aligned with the *M. punctulatus* section of the subgenus rather than with *M. dolomieu,* because the counts are relatively low for the soft rays of the dorsal, anal, and pectoral fins and for the scale rows along, above, and below the lateral line, and also because the color pattern is more like that of the *M. punctulatus* series than that of *M. dolomieu.*

The lateral-line scale count, which is lower than in any form of the subgenus except *M. p. punctulatus,* is notably less than in *M. d. dolomieu, M. d. velox,* and *M. p. henshalli,* and slightly overlaps the count of *M. coosae,* of *M. p. treculii,* and of *M. p. wichitae.* The ventrolateral longitudinal dark streaks, so characteristic of subadult examples of the *coosae–punctulatus* complex, are very imperfectly developed, and rather regularly aligned only on the caudal peduncle. The shallowly emarginate dorsal fin, the deep body (especially of the young), and the vertical elongation of lateral blotches are reminiscent of these features in *M. coosae* and in *M. d. dolomieu;* the prominent basicaudal spot and the broadened lateral blotches (which are often fused) are suggestive of *M. punctulatus.* The soft dorsal, caudal, and anal fins of the young are more boldly mottled and spotted than in any other form, but the strong caudal band, characteristic of the young of all species except *M. coosae* and *M. salmoides,* is not well formed in the 2 fingerlings of *M. notius.* The bright blue on the lower anterior parts in life seems to be unique for the genus.

Types.—The holotype (U.M.M.Z., No. 134628), a fingerling 67.7 mm. in standard length and 84.5 mm. in total length, was collected by Archie F. Carr, Jr., on September 24, 1941, at the head of Ichtucknee Springs, Columbia County, Florida.

Five paratypes: U.M.M.Z., No. 134629 (3), taken with the holotype, and U.M.M.Z., No. 147193 (2), speared by E. Ross Allen and W. M. McLane while goggling in Ichtucknee Springs on April 9–10, 1941.

HABITAT.—Ichtucknee Springs discharge into the Santa Fe River of the Suwannee River system. They lie 5 miles northwest of Fort White, in the northwestern quarter of section 7, Township 6 South, Range 16 East. Cooke (1939: 97, Fig. 49) illustrated the main spring (spelled by him Itchatuchnee) and reported that it issues as a strong boil through the Ocala Limestone. One of the larger springs of Florida, it has a reported flow of more than 400 second feet and a temperature of 74° F.

DESCRIPTION.[2]—The form is robust; greatest depth, 3.2. The caudal peduncle is relatively deep and short, but becomes more attenuate with age; least depth, 8.0; length, 4.9. The body is moderately compressed; greatest width, 6.0. Head large, its length, 2.6; relatively smaller with age. The dorsal fin has a rather shallow emargination, which becomes less marked with age; the ninth and shortest spine is 59.7 per cent of the fourth and longest (1.67 in longest); fourth spine, 9.4. The spinous dorsal becomes progressively lower with age. In the holotype the fifth spine is abnormal, divided to its base. As is usual in the subgenus, the soft dorsal and anal each have small scales on the interradial membranes near their bases. Both fins are smoothly rounded, and each becomes somewhat lower with increased age. The longest soft dorsal ray is usually slightly higher than the longest anal ray, but in the holotype each measures 6.0. The 3 graduated anal spines become relatively shorter with age; the third and longest is 9.9 in standard length. The pectoral fin is short and rounded distally; length, 5.2. The pelvic fin is of moderate length, but becomes relatively shorter with age; length, 5.35.

[2] Measurements of the holotype, as given in the description, were taken with dividers. Fin-ray and scale counts and proportional measurements for each of the 6 specimens are given in Table I. The methods of counting and measuring used in this paper are the same as those employed by Hubbs and Bailey (1940: 9–10).

The caudal fin is very shallowly emarginate, and the lobes are rounded; length from base to tip of longest ray, 4.0; length to tip of median ray, 5.2 (1.27 in caudal length). Tip of snout to origin of dorsal, 2.25; tip of lower jaw to insertion of pelvic, 2.6; thence to origin of anal, 3.5.

Width of head, 2.15 in head length. The predorsal contour, scarcely curved in the smaller specimens, becomes weakly sigmoid in the adult (Pl. I). In the profile of the head and body, except for the weaker emargination of the dorsal fin, *M. notius* bears a very striking resemblance to *M. salmoides.* The snout is relatively shorter than in other species of the subgenus *Micropterus;* length, 4.0. The orbit, as usual, becomes much smaller with age; length, 4.2. The flat interorbital becomes broader with age; least bony width, 5.7. The maxilla extends to below the posterior margin of the pupil (below posterior margin of orbit in adults); length of upper jaw, 2.1. The lower jaw projects slightly; length, 1.7, increasing with age.

Dorsal, X, 12; anal, III, 10; pectoral, 16–15 (16–16 in five paratypes). Scales, 8 or 9—59 to 63—16 to 19; 27 to 29 rows around caudal peduncle and 10 to 15, usually 12 or 13, rows on cheek. Scales are well developed on the opercle, subopercle, and interopercle. Those of the opercle are not much larger than those on the cheek. The few scales on the preopercle are imbedded. In the 1 paratype counted the vertebrae number $14 + 18 = 32$.

The bony margins of the lachrymal, suborbitals, preopercle, and the opercular bones are entire. The branchiostegal rays number 6–6 in all 6 specimens. The opercle terminates posteriorly in 2 flat, blunt, rigid projections, of which the lower is much the longer.

The dentaries and premaxillae bear broad bands of depressible villiform teeth. The head of the vomer has a triangular patch, and the palatine has an elongate band of villiform teeth. The ectopterygoid has smaller teeth than the palatine. A subcircular patch of glossohyal teeth is present in each specimen. The gill rakers number $2 + 6$ and $2 + 5$ in the holotype; the count is usually 2 + 5, occasionally 1 + 5, 2 + 4, or 2 + 6. In 2 paratypes the pyloric caeca number 10 and 13; all are simple, except for 1 that is branched at its base in 1 specimen and for 1 that is forked about a third of its length from the distal tip in the other.

In coloration, as well as in body form, *M. notius* strongly resembles *M. salmoides.* The body is marked with a series of about 12 lateral blotches. These are vertically elongate, as in *M. dolomieu* and *M. p. treculii,* but anteriorly are much wider than the interspaces and on the caudal peduncle fuse to form a relatively uniform lateral band. They are not light-centered. The basicaudal spot is large. In the smaller specimens it is blackish and is bordered by a light area that is framed by a subtriangular dark mark (Pl. I, Fig. 1). Ventrolateral dark streaks are weakly developed, rather definite only on the caudal peduncle of the 4 largest specimens. In the larger adults the fins are uniformly dusky or show an obscure pattern of mottles, but in the 2 fingerlings the soft dorsal, caudal, and anal are clearly spotted or suffused with dark on a light ground color. In the 2 smaller adults the basal parts of the soft vertical fins are finely mottled and reticulated with light and dark and the caudal fin is darker than in other forms of *Micropterus* at the same size; the basal part is not evidently light, the subterminal dark band across the caudal lobes is less well marked, and the lobes are narrowly edged with light. As usual in the genus there is a black spot on the posterior part of the opercle and 3 brownish oblique lines cross the cheek, backward and downward from the eye.

Striking as the color pattern of preserved specimens may be, the life colors must be even more impressive. One of the collectors of the 2 small adults, William M. McLane, reported that the brilliantly colored nesting fish, taken on April 9 and 10, attracted his attention because the cheeks, breast, and ventral parts of the sides were turquoise blue. These fish were much brighter, he added, than any smallmouths (*M. d. dolomieu*) that he had seen in Lake Erie.

Relationships.—Among the species of the subgenus *Micro-*

pterus, notius presents the closest structural approach to the subgenus *Huro* (*Micropterus salmoides*), as is evidenced in the coloration, in body form, and in the size of the scales (especially on the cheek and along the body). These *salmoides*-like features, in addition to other evidence, suggest strongly that *notius,* more than any other species, retains a generalized position in the genus close to the prototypic *Micropterus.* From some such ancestor as *M. notius* differentiation has proceeded along 2 independent lines. The bifurcate caeca and the deeply incised dorsal fin of *salmoides* are believed to represent specializations along 1 evolutionary line (*Huro*). Progressive differentiation in the other main line, in the subgenus *Micropterus,* has been characterized, among other features, by a reduction in scale size, by pattern evolution, and by modification of body form. A parallel change from the presumably primitive vertebral count, 14 + 18 = 32, to 15 + 17 = 32, probably arose independently in each of the 2 principal evolutionary lines, terminated by *salmoides* and *dolomieu,* respectively. Similarly, a trend toward reduction in dentition (especially of the glossohyal) has occurred both in *salmoides* and in *dolomieu.*

We have entertained but rejected the idea that the bass from Ichtucknee Springs may be hybrids between *M. salmoides* and some species of the subgenus *Micropterus.* General appearance favors this concept, but other considerations contradict it. In the first place, no other form of the subgenus *Micropterus* seems to occur in or near Ichtucknee Springs. In the second place, hybridization between the species of *Micropterus* is extremely rare[3] and no hybrid between the sub-

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[3] In addition to the 3 hybrid specimens reported previously (Hubbs and Bailey, 1940: 39–40), we have recognized only 1 other (U.M.M.Z., No. 131545), a yearling specimen 106 mm. in standard length. It is identified as *Micropterus dolomieu* (*dolomieu* × *velox*) × *M. punctulatus punctulatus.* It was collected in White River one-half mile northeast of Wyman, Washington County, Arkansas, by J. D. Black and Henry Mills on July 27, 1940. Its main counts are: dorsal, IX, 14; anal, III, 10; pectoral, 15–16; scales, 9—65—15, with 26 rows around the caudal peduncle and 17 rows on the cheek.

TABLE I

PROPORTIONAL MEASUREMENTS AND COUNTS ON 6 TYPES OF *Micropterus notius*, AND ON 1 SPECIMEN OF *Micropterus* SPECIES FROM THE CHIPOLA RIVER, MARIANNA, FLORIDA

The U.M.M.Z. catalogue numbers for the *M. notius* specimens are Nos. 134629 (1 and 2), 147193 (3 and 4), 134629 (5), and 134628 (6, the holotype)

Character	*Micropterus notius*							*Micropterus* Species
	1	2	3	4	5	6	Mean	
Standard length (mm.)	218.5	190.5	181.0	176.5	75.0	67.7	151.5	313
Thousandths of standard length								
Head length	384	378	360	371	388	390	379	342
Greatest depth	336	329	318	312	327	323	324	297
Least depth	130	128	133	125	133	130	130	110
Body width	....	197	177	159	176	168	175	174
Caudal peduncle length	240	226	227	218	220	210	224	233
Pectoral length	194	202	191	195	207	198	198	172
Pelvic length	176	181	177	171	195	191	182	150
Highest dorsal spine	94	87	84	87	113	106	95	75
Lowest dorsal spine	63	55	56	55	67	64	60	40
Highest dorsal soft ray	167	168	169	161	181	171	170	144
Highest anal spine	89	76	84	83	97	103	89	50
Highest anal soft ray	156	156	156	154	180	171	162	136
Head width	....	542	519	498	488	458	501	500
Orbit length	193	199	216	213	241	242	217	176
Interorbital width	211	199	199	193	179	182	194	230
Snout length	259	263	262	268	261	261	262	285
Upper jaw length	483	476	486	483	467	462	476	486
Lower jaw length	598	588	597	596	588	576	591	605

TABLE I (*Cont.*)

Character	*Micropterus notius*							*Micropterus* Species
	1	2	3	4	5	6	Mean	
Thousandths of length of highest dorsal spine								
Lowest dorsal spine	665	636	664	634	588	597	631	528
Counts								
Dorsal spines	10	10	10	10	10	10	10.00	10
Dorsal soft rays	12	12	12	12	12	12	12.00	11
Anal soft rays	10	10	10	10	10	10	10.00	10
Pectoral rays*	16–16	16–16	16–16	16–16	16–16	16–15	15.92	16–16
Scales above lateral line*	9–8	8–8	8–8	9–9	–8	8–8	8.27	10
Scales along lateral line*	60–60	63–62	61–59	63–	59–59	62–61	60.82	77
Scales below lateral line*	16–17	17–17	18–17	19–18	17–18	17–18	17.42	20
Scales around caudal peduncle	27	28	29	28	28	27	27.83	31
Scale rows on cheek*	14–12	13–15	13–12	13–12	11–12	11–10	12.33	14

* Counts recorded for both sides, except on the specimen from Chipola River.

genera has been encountered. In the third place, certain characters are inconsistent with the hybridization theory. For example, the notch between the dorsal fins is much shallower than would be expected of a hybrid involving *M.* (*Huro*) *salmoides* as 1 parent. Other characters do not display the intermediacy that one comes to expect in fish hybrids.

We interpret *M. notius* as an endemic species in the sinkhole region of northern Florida and probably as a relict, since it seems to be the most generalized species of the genus. In the same region there is a largely subterranean form of the minnow *Erimystax harperi* (Fowler) and the stream form, *E. h. harperi,* centers here, as do also a genus and species of darter, *Villora edwini* Hubbs and Cannon. A few other fishes seem to find in this region the center of their restricted range. Here also are distinct species of crayfish (Hobbs, 1942) and ferns (St. John, 1936).

The name *notius* is from *νότος*, "southern."

II

THE SPOTTED BASS, *Micropterus punctulatus*, IN FLORIDA

We have previously shown that *Micropterus punctulatus henshalli* of the upper parts of the Alabama and Tombigbee river basins is represented in southern Alabama, southern Mississippi, and extreme southeastern Louisana by a population intermediate between *M. p. henshalli* and the widespread *M. p. punctulatus* (Hubbs and Bailey, 1940: 16, Map 1, Tables V and VI). The expected extension of the area of intergradation into extreme western Florida is now confirmed.

The following Florida collections of *Micropterus punctulatus: henshalli* × *punctulatus* are in the Museum of Zoology:

No. 134626 (6 specimens, 46.5 to 68.5 mm. in standard length), collected in the Escambia River, west of Jay, Escambia County, October 12, 1941, by A. F. Carr, Jr. The lateral-line scales number 65 in 1 specimen, 66 in 4, and 68 in 1; the scale count around the caudal peduncle is 25 in 3 and 26 in 3.

No. 134601 (1 specimen, 110 mm. in standard length), collected in Perdido Creek, near Pineville, Escambia County, October 12, 1941, by Carr. The lateral-line count is 63, and there are 24 scales around the caudal peduncle.

No. 147187 (3 specimens, 65 to 153 mm. in length), collected in Sweetwater Creek, near Munson, Santa Rosa County, April 11, 1941, by Carl L. Hubbs and Boyd W. Walker. The lateral-line scale counts are 62, 68, and 70 and the caudal peduncle counts are 23, 24, and 24.

The mean values for the 10 specimens are 66.0 for lateral-line scales and 24.8 for scale rows around the caudal peduncle. The 26 intergrades reported previously have values of 66.54 and 25.08. The averages for *M. p. henshalli* have been determined as 72.26 and 27.55, respectively, and for *M. p. punctulatus* as 63.71 and 24.44 (Hubbs and Bailey, 1940: 49–50).

Two specimens of *Micropterus punctulatus,* taken by A. F. Carr, Jr., on October 13, 1941, in the mouth of the Flint River, Apalachicola River system, Gadsden County, Florida, far to the east of other records of the species along the Gulf coast, cannot be identified as intergrades. The 2 specimens have lateral-line scale counts of 62 and 63 and the caudal peduncle rows number 23 and 25. These values are at or near the lower limit of variation for intergrades between *henshalli* and *punctulatus,* but are near the modal counts for the typical subspecies. In view of the absence of other records of the species in the Apalachicola system, and because of the phenotypic agreement of these specimens with the typical subspecies, they are provisionally identified as *M. p. punctulatus.* If this determination is correct, it is highly probable that the population at this locality is the result of stocking. We have no information regarding plantings of this species in Florida, but at least 1 journalist has advocated its wide dissemination in the state.

III

A BASS, *Micropterus* SPECIES, FROM THE CHIPOLA RIVER

In 1940 we reported (Hubbs and Bailey, pp. 6. 28, Map 1), but did not identify, a large specimen of *Micropterus* (U.M.M.Z., No. 110997) from the Chipola River in the Apalachicola system at Marianna, Jackson County, Florida. On our recommendation, based on preliminary study of this specimen, Carr (1937: 85) had previously included *Micropterus pseudaplites* (= *punctulatus*) in the list of Florida fishes. The specimen was collected by O. C. Van Hyning on January 27, 1933, and there seems to be no reason to question its provenance. A rock bass, *Ambloplites rupestris ariommus*[4] Viosca, taken from its stomach, supports the locality record, since from southern Louisiana to southwestern Georgia that subspecies is strictly coastwise in its distribution.

Since our initial report of this interesting fish, we have collected independently at and near Marianna in a futile effort to secure additional material, and several other collectors have tried to obtain specimens there with no more success. Since high water restricted our field activities, our failure to capture specimens constitutes no proof that the bass is rare at Marianna. Some local residents may well have had this species in mind in speaking of a relatively small-mouthed form known as "shoal bass," which is more active than the largemouth when hooked and more apt to leap in its struggles to escape.

Although we continue to hold in abeyance a determination of the Chipola bass, we strongly suspect that it represents an undescribed form. In this connection it should be recalled that the region of the Chipola River has been found to be one of rather high endemism. For example, Carr and Marchand (1942) described from this stream a distinct species of turtle. The naiad fauna of the Chipola River is marked by high endemism (van der Schalie, 1940). Two endemic darters, *Doration davisoni* (Hay) and *Poecilichthys okaloosae* (Fowler), inhabit western Florida, along with 5 or more undescribed species of fishes.

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[4] Specimens of *Ambloplites* in the Museum of Zoology from the lowlands of eastern Arkansas and southeastern Missouri are clearly intermediate between *ariommus* and *rupestris; ariommus* is therefore regarded as a subspecies of *rupestris.* Fowler's recent action (1945: 253) in naming a genus *Bartramiolus,* for the sole reception of *Ambloplites ariommus* Viosca is thus seen to be wholly unwarranted. *Bartramiolus* Fowler is herewith relegated to the synonymy of *Ambloplites* Rafinesque; the type species of these nominal genera are conspecific.

On the basis of the low fin-ray counts, the low count of scales above the lateral line, and proportional measurements (Table I, last column), as well as the color pattern, the Chipola bass is clearly allocated to the *punctulatus* section of the subgenus *Micropterus* (also including *coosae* and *notius*), as opposed to the *dolomieu* group. It is sharply differentiated from *notius,* as well as from *M. p. punctulatus, M. p. treculii,* and *M. p. wichitae,* by the small scales, among other characters. The counts for the lateral-line scales (77) and for the rows around the caudal peduncle (31) contrast with the maxima in those forms of 72 and 29, respectively. It is from a geographic locality remote from all of these except *notius* (see record of presumed introduction of *M. p. punctulatus,* p. 11). *M. coosae* and *M. p. henshalli* are the nearest geographical representatives of the genus and have the closest structural similarity. In all scale counts (Hubbs and Bailey, 1940: Tables V and VI), except for the number of rows on the cheek, the Chipola bass equals or slightly exceeds the maxima for these forms. The 31 scales around the caudal peduncle contrast with the mean of 27.55 (maximum, 29) in *M. p. henshalli* and of 28.34 (maximum, 31) in *M. coosae.* Although parallel variations have been noted in *M. coosae* from the Black Warrior River system in Alabama (Hubbs and Bailey, 1940: 28), identification with that form would seem to be precluded by reason of the greater emargination of the dorsal fin in the Chipola bass: the lowest dorsal spine is 52.8 per cent of the highest, as opposed to 70.7 per cent (61.7–77.2) in typical *M. coosae.* Furthermore, there are no glossohyal teeth, whereas these teeth are absent in only 2 of 22 examples of *M. p. henshalli* and in 9 of 42 specimens of *M. coosae* examined. There are 10 pyloric caeca, all unbranched. The large size of the Chipola bass (over-all length, 388 mm., as against 203 mm. and 261 mm., respectively , for the largest *M. p. henshalli* and

M. coosae specimens examined), prevents a comparison at equivalent sizes, but the color pattern is more reminiscent of *M. p. henshalli* than of *M. coosae*. *M. coosae* occurs in the upper and middle Chattahoochee system, but (except for the presumably introduced *M. p. punctulatus*) no representative of *punctulatus* is known from the Chattahoochee–Apalachicola basin. Since the Chipola bass does not seem identifiable with *coosae* as represented in the drainage, the geographic as well as the structural implications suggest alignment with *M. punctulatus,* but in the absence of more material we do not venture a decision as to whether it is a variant *henshalli,* represents an undescribed subspecies of *punctulatus,* or presages recognition of a wholly distinct species. As already stated we lean to the belief that it belongs to an undescribed form.

IV

HAS THE SMALLMOUTH BASS, *Micropterus dolomieu,* BECOME ESTABLISHED IN FLORIDA?

The smallmouth bass has long been regarded by sportsmen and writers on game fishing as an exotic inhabitant of certain lakes in the vicinity of Oakland in central Florida. *Field and Stream* magazine credits Lake Apopka, near Oakland, with the production of the record smallmouth, a 14-pound specimen, 28 inches long and 21¼ inches in girth, caught by Walter Harden on February 9, 1932. This supposed record has been mentioned in several pamphlets and books, for example by LaMonte (1945: 174). Several other fish nearly as large, taken in the same or in near-by lakes, have been accorded considerable publicity. Without having any firsthand evidence, Carr (1937: 85) and Hubbs and Bailey (1938: 29, 52) accepted these accounts as reliable. The Florida Game and Fresh Water Fish Commission included the species in an anonymous account of the game fish of the state (1946: 6–7).

Belief that the smallmouth is established in Florida has apparently been based on the known introductions of northern stock by the United States Bureau of Fisheries (and perhaps other agencies), and by identifications of large fish taken subsequently. These determinations have been made not only by anglers but by ichthyologists.

For some time we have been sceptical of the reported success of plantings of the northern smallmouth in Florida. Our own collections have not included the species. Neither have those of Archie F. Carr, Jr., and his active associates at the University of Florida. O. Lloyd Meehean, chief of the Division of Game-fish and Hatcheries of the United States Fish and Wildlife Service, who for several years was stationed in Florida, informed us (letter of July 9, 1946) that he has never seen a smallmouth bass from Florida. He wrote:

> I tried to run down two or three reports of smallmouth bass without success. At Winter Haven they reported smallmouth in the city lake and upon investigation I found that these were merely largemouth which were stunted as a result of over-population or possibly lack of food so that the size and shape had been considerably changed, but they were still typical largemouth.

Mr. Herb Mosher, angler and prolific outdoor writer of the *Orlando Morning Sentinel*, has in his column repeatedly raised the question of the occurrence in Florida of the smallmouth. Despite pages of newsprint devoted to the controversy and numerous pleas for specimens, none has been forthcoming. He does not believe that the smallmouth occurs in Florida. Photographs and mounted specimens of several large Florida bass reputed to be smallmouths, including one from Lake Tsala Apopka approximately as large as the accepted world record, have been made available to us, but all of these have proved to be largemouths. In short, despite the unquestioned fact that the species has been planted, we can find no valid evidence that the smallmouth has become established in Florida waters.

Why then have ichthyologists identified record-sized fish as smallmouth? The answer to this question is as simple as it is unexpected. Current descriptions and keys, our own included (Hubbs and Bailey, 1938: 14–15; 1940: 10–13), compare northern smallmouths with northern (not Florida) largemouths. It is now evident that the peninsular largemouth parallels the smallmouth in certain characters commonly used for identification, both forms contrasting in these respects with the northern *salmoides*.

The undue reliance placed on scale counts is apparently chiefly responsible for the misidentifications. In *M. d. dolomieu* there are 68 to 81 (usually 72 to 77) lateral-line scales, and in northern *salmoides* 58 to 69, usually 61 to 66. The peninsular largemouth, however, has 65 to 75, usually 69 to 73. Whereas *M. d. dolomieu* has 14 to 18 (usually 15 or 16) rows of scales on the cheek, northern specimens of *salmoides* have 9 to 12, usually 10 or 11. But the largemouth from peninsular Florida has from 10 to 14 (usually 11 to 13).

Mounted specimens in particular are difficult to identify, because of the loss, misrepresentation, or distortion of such important characters as coloration, pyloric caeca, size of mouth, and body form. We believe that the difficulties attending the identification of mounted examples or skins (in contrast to properly preserved museum specimens), along with the small size of the scales in Florida largemouths, adequately account for the incorrect determinations. We conclude that there is no valid evidence that *Micropterus dolomieu* is established in Florida. Characters such as the structure of the pyloric caeca, the relative lengths of shortest and longest dorsal spines, pectoral-ray count, and color pattern (Hubbs and Bailey, 1940: 10–13) should be relied upon for the differentiation of these species.

We therefore recommend the removal of Florida fish from consideration for the title of "world's record" smallmouth bass. We leave to others the decision as to what fish properly deserves the distinction of holding the record, but stress here the importance of accurate identification.

V

THE SCIENTIFIC NAME OF THE LARGEMOUTH BASS

The early history of the changes in the scientific name of the largemouth bass need not be recounted at length. Henshall (1881: 110–32) finally clarified the situation, and except for the unjustified reversion to the specific name *floridana* by certain recent authors, the name *salmoides* has been in general use since that time. Disagreement in nomenclature during recent years has centered largely on the proper generic allocation.

At a time when only 2 species of black bass were recognized, Hubbs (1926: 69, 71) called attention to the many striking differences between them, noting especially the trenchant features of the simple or bifid pyloric caeca, the scaled or scaleless base of the anal and soft dorsal fins, and the shallowly emarginate dorsal as contrasted with the almost separate dorsal fins. The character differences were regarded as worthy of generic separation, and the name *Aplites* was associated with *salmoides.*

Although the sharpness of the distinction was lessened when 4 species and 7 forms of black bass were recognized (Hubbs and Bailey, 1940), the largemouth bass was still accorded generic status. The name *Huro* was adopted for its genus, since, on reconsideration of Rafinesque's names, *Aplites* was interpreted as a strict synonym of *Micropterus.*

Several of the characters that separate *M. salmoides* and *M. dolomieu* break down when the 5 species and 10 forms that we now recognize are critically compared. As noted on page 7, *M. notius* approaches *M.* (*Huro*) *salmoides* more closely in several respects than does any other species of the subgenus *Micropterus.* In the emargination of the dorsal fin *M. punctulatus* is intermediate between *M. salmoides* and *M. dolomieu,* and scales are commonly present on the preopercle (earlier regarded as an exclusive feature of *M. salmoides*). The mouth in several of the newly recognized forms, though smaller than in *salmoides,* is much larger than in *M. dolomieu.* The size of the cheek scales varies among the species so much that this character is of no value in separating the groups. The body form of *M. notius* is strikingly similar to that of *M. salmoides,* and in general features of coloration *M. notius* and *M. punctulatus* bear even closer resemblance to *M. salmoides* than to

M. dolomieu. The presence of scales on the fin bases in *Micropterus, sensu stricto,* usually serves as a clear-cut differentiating feature, but some specimens of *M. salmoides* have a few isolated scales near the bases of the anal and soft dorsal fins. There remains the character of the simple pyloric caeca in *Micropterus,* contrasting with the branched caeca in *Huro.* But, as already noted, some of the caeca are unbranched in *Huro,* and, as now verified by us for *M. notius,* 1 or 2 of the caeca are branched in some specimens of the species of the subgenus *Micropterus.* There seems to be little doubt that *Micropterus* and *Huro* are natural groups and that *salmoides* represents a structural type distinct from *Micropterus.* Whether 1 or 2 genera should be recognized is a matter of opinion.

Since our 1940 revision, several workers, including De Buen (1941), have disagreed with the retention of 2 genera. We now recognize *Huro* as a subgenus of *Micropterus* because of the close resemblance of certain species of *Micropterus* to *Huro,* the gradation from one extreme to the other in most of the characters which have formerly been used for separation, and the difficulty in evaluating the importance of the other characters. The name of the largemouth bass may stand as *Micropterus* (*Huro*) *salmoides* Lacépède.

VI

THE SUBSPECIES OF *Micropterus salmoides*

As already mentioned, we recognize the largemouth bass of peninsular Florida as a distinct subspecies, which intergrades geographically with the northern form. We thus confirm an earlier suggestion (Hubbs and Bailey, 1940: 39) that *M. salmoides* is not a single unit. The Florida subspecies and the intergrades are discussed below.

We tentatively refer all bass from north and west of the range of the intergradation to the typical subspecies, *M. s. salmoides,* although we suspect that one or more additional subspecies may prove recognizable when adequate studies have been made. The largemouths in the southwestern extremity of the natural range of the species may prove separable on the basis of a high incidence of glossohyal teeth. These teeth are almost invariably absent in *M. s. floridanus* (p. 30), are lacking in 52 out of 58 examples from South Carolina (topotypical *salmoides*), and are seldom developed in northern specimens. If a southwestern subspecies should be recognized, the name *nuecensis* (*Grystes nuecensis* Baird and Girard, 1854) may be available for it.

There are less definite indications that still other forms may exist. Thus, some specimens from the Atlantic coast drainages of Georgia, South Carolina, and North Carolina exhibit in part or to some extent the coloration of *M. s. floridanus,* although they do not have the high scale counts of that form. Some adults from South Carolina disagree with northern largemouths in the size of the mouth. It is the belief of Mr. Percy Viosca, Jr., that a different type of *M. salmoides* occurs in the Ouachita River and its tributaries in north Louisiana (personal communication).

NORTHERN LARGEMOUTH BASS

Micropterus salmoides salmoides Lacépède

The typical subspecies of the largemouth is known to occur in Florida in pure form only in the Pensacola Bay drainage in the western part of the Panhandle. The records by Goode and Bean (1879 : 138), under the name *Micropterus pallidus,* for Pensacola, and of Bollman (1886 : 464), as *Micropterus salmoides,* from near the mouth of the Escambia River, are referable to the typical subspecies. The counts for the Pensacola Bay drainage recorded in Tables II to VII were taken from 2 series, with data as follows : U.M.M.Z., No. 144583, 3 specimens, 51 to 76 mm. long, collected by Reeve M. and Marian K. Bailey on August 21, 1939, in Pond Creek, about 2 miles southwest of Milton, Santa Rosa County, Florida ; U.M.M.Z., No. 88699, 8 fish, 41 to 105 mm. long, seined by Herbert R. Becker and Edwin P. Creaser on September 16, 1929, in a high-water pond of Conecuh River, 8 miles west of Troy, Pike County, Alabama. Another specimen, 54 mm. long, was collected by Carl L. and Laura C. Hubbs and Boyd W. Walker on April 11, 1941, in Big Escambia Creek, at Flomaton, Escambia County, Alabama.

FLORIDA LARGEMOUTH BASS

Micropterus salmoides floridanus (LeSueur)

Cichla Floridana.—LeSueur, 1822: 219–20 (original description; east Florida).

Micropterus floridanus.—Jordan and Copeland, 1876: 137 (in part; Florida).

Huro floridana.—Jordan, Evermann, and Clark, 1930: 297 (in part; Florida). Schrenkeisen, 1938: 237–40 (in part; Florida).

Micropterus salmoides floridanus.—McLane, 1948: 103–38 (near Welaka; food).

Grystes salmoides (incomplete identification).—Holbrook, 1860: 28–31 (in part; records from Florida).

Micropterus salmoides.—Henshall, 1881: 110–11, 135–74 (in part; Florida records). Goode, 1884: 401–4 (in part: St. John's River; Gainesville;[5] size). Henshall, 1889: 22–29, 41–44, 53 (in part; St. John River; rivers issuing from large clear springs, Hernando County; size). Henshall, 1891: 386 (Myakka and Hillsborough rivers and tributaries, in fresh and brackish water). Bollman, 1891: 577–78 (in part; Florida). Woolman, 1892: 297–98 (localities in Peace and Hillsboro river drainages). Lönnberg, 1894: 125–26 (St. John's River and lakes, including Lake Apopka; color). Jordan and Evermann, 1896: 1012 (in part; Florida). Evermann and Bean, 1898: 243 (Eau Gallie Creek and South Lake, tributaries to Indian River). Evermann and Kendall, 1900: 72 (literature reports; Palatka, Welaka, Match Creek, tributary to Ocklawaha River, and Lake Monroe). Henshall, 1908: 18–20 (in part; size attained in Florida). Fowler, 1915: 249 (West Palm Beach and Lake Kerr). Fowler, 1923: 30 (Bayport, Lake Okeechobee and Caloosahatchie River). Pratt, 1923: 120–21 (in part; Florida). Fowler, 1926: 252 (Lake Trafford). Harkness and Pierce, 1941: 112 (Lake Mize).

Micropterus salmonoides (emended spelling).—Boulenger, 1895: 16–18 (in part; Wekiwachee River).

Aplites salmoides.—Hubbs, 1927: 6 (Florida; characters; *Cichla floridana* regarded as a synonym). Mueller, 1936: 807–8 (host of copepod parasites; Myakka River near Sarasota and canals of Lake Okeechobee near Clewiston).

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[5] All definite localities mentioned in this synonymy are in Florida.

Huro salmoides.—Jordan, 1929: 145–46 (in part; Florida). Pratt, 1935: 114 (in part; Florida). Carr, 1937: 85 (characters). Hubbs and Bailey, 1938: 15, 18–19 (in part; Florida). Bangham, 1939: 265 (parasites; near Englewood, Peace River tributaries, Myakka River, Lake Okeechobee). Hubbs and Bailey, 1940: 13, 37–39 (in part; Florida; partial synonymy). Fowler, 1941: 240–41 (St. John's River; mouth of Blue Springs Run, Volusia County; Lake Okeechobee; Wekiva Springs, near Apopka, Orange County; Lake Apopka; Orange Lake; Fannin and Manatee springs, Levy County [possibly intergrades]; Salt Springs, west of Lake George; Silver Glen Springs, Marion County). Bailey, 1941: 6 (Mill Dam Lake, Marion County). M. H. Carr, 1942: 43–77, Pls. 7–12 (breeding habits and embryology; Bivens Arm, 3 miles south of Gainesville; St. John's River). Meehean, 1942: 184–94 (populations; Clearwater, Buck and Big Prairie lakes and First and Little Deep ponds, Ocala National Forest). Hubbs and Allen, 1944: 125 (Silver Springs; characters; habits). Allen, 1946: 27, fig. (Silver Springs; habits). Fowler, 1945: 298 (Punta Gorda, Alligator River tide ditch; Boggy Creek, Nassau County; Boca Raton, Palm Beach County).

Micropterus pallidus (not of Rafinesque).—Jordan, 1880*a:* 19 (San Sebastian River, tributary to Indian River; no lingual teeth). Jordan, 1880*b:* 22 (St. John's River). Bean, 1880: 96–97 (St. John's River; Jacksonville). Earll, 1887: 529 (St. John's River).

Largemouth black bass.—Meehean, 1944: 220–30, Figs. 1–2 (gain in weight as measure of production; hatchery at Welaka, fed from St. John's River).

There appears to be no doubt as to the applicability of LeSueur's name (*Cichla Floridana*) to the large mouth bass of peninsular Florida. Originally described from east Florida, it may be assumed that the specimens came from the St. Johns River system, in which this subspecies is common.

DIAGNOSIS.—A form which agrees in most characters with *Micropterus* (*Huro*) *salmoides salmoides*, but differs in the smaller scales (Tables II–VIII), in the larger maximum size attained, and in coloration. There are 10 to 14 (usually 11 to 13) rows of scales on the cheek, 7 to 10 (usually 8 or 9) rows above the lateral line, 65 to 75 (usually 69 to 73) scales along the lateral line, 16 to 18 (usually 17 or 18) rows below the lateral line, and 27 to 32 (usually 28 to 31) rows around the caudal peduncle. A character index for scale size (derived by summing the number of rows of cheek scales, the number of scale rows above and below the lateral line, the number of scales along the lateral line, and the number of rows around the caudal peduncle) gives values of 129 to 145 (usually 135 to 142; 131 or more in 97 per cent of the 72 individuals examined).

According to our scale counts (Tables II–VII) it is possible to set lines that permit separation of most of the specimens of *floridanus* from most of those of *M. s. salmoides,* except in the belt of intergradation. Only for the count of scales above the lateral line does the "per cent identifiable" fall below the 75 per cent level that is customarily recognized as indicative of subspecific differentiation. For the different counts the percentages (Table VIII) are as follows: rows of scales on cheeks, 84 per cent of *M. s. floridanus* separable from 82 to 100 per cent of the several sets of *M. s. salmoides;* scales above lateral line, 55 per cent separable from 87 to 100 per cent; scales along lateral line, 96 per cent from 83 to 93 per cent; scales below lateral line, 78 per cent from 85 to 100 per cent; scales rows around caudal peduncle, 75 per cent from 95 to 100 per cent; meristic index, 97 per cent from 97 to 100 per cent.

The larger size attained by the Florida largemouth, as compared with the northern subspecies, has long been recognized and has stimulated speculation regarding the cause (Hubbs, 1932: 88). Since this form is now shown to be distinguishable morphologically, it seems probable that the large growth potential has in part a genetic basis. Without knowledge of our proposed separation of the subspecies, J. Sanford Hart has informed us that in the physiology of lethal temperatures the largemouth bass of the Tennessee River system (typical *salmoides*) resembles the Lake Erie population more than it does the Florida bass.

TABLE II

Subspecific Differentiation and Intergradation of *Micropterus salmoides* in Number of Rows of Scales on Cheek

Subspecies and Drainage Basins	Spec-imens	Total Range	Usual Range	Mean	SD	SE	Percentages	
							9–11	12–14
M. s. salmoides								
Great Lakes and Mississippi River	43	9–13	10–11	10.44	.87	.13	86	14
Mobile River	15	9–12	9–11	10.20	.83	.22	93	7
Big Lake, Ala.	22	9–12	10–11	10.86	.76	.16	82	18
Pensacola Bay	10	9–11	10–11	10.10	.57	.18	100	0
Intergrades								
Choctawhatchee and St. Andrews bays	5	10–14	10–13	12.00	1.23	.55	40	60
Apalachicola River	11	10–12	10–12	11.09	.83	.25	64	36
Ochlockonee River	5	10–14	11–14	12.20	1.64	.73	40	60
Fenholloway River	20	10–13	10–12	11.15	1.00	.22	65	35
Suwannee River	19	9–13	11–13	11.47	1.31	.30	47	53
M. s. floridanus								
Florida peninsula	73	10–14	11–13	12.27	.88	.10	16	84
Intergrades								
Nassau and St. Marys rivers	10	9–12	11–12	11.10	.99	.31	60	40
Satilla River	20	9–12	10–11	10.60	.83	.19	85	15
Altamaha River	7	10–11	10–11	10.43	.56	.21	100	0
Savannah River	11	10–12	10–12	11.09	.83	.25	64	36
M. s. salmoides								
South Carolina north of Savannah River	77	9–12	10–11	10.34	.83	.09	94	6

TABLE III

SUBSPECIFIC DIFFERENTIATION AND INTERGRADATION OF *Micropterus salmoides* IN NUMBER OF SCALES ABOVE LATERAL LINE

Subspecies and Drainage Basins	Specimens	Total Range	Usual Range	Mean	SD	SE	Percentages	
							7–8	9–10
M. s. salmoides								
Great Lakes and Mississippi River	46	7–9	8	7.93	.48	.07	91	9
Mobile River	15	7–9	7–8	7.73	.71	.18	87	13
Big Lake, Ala.	22	7–8	7–8	7.59	.51	.11	100	0
Pensacola Bay	10	7–8	8	7.90	.32	.10	100	0
Intergrades								
Choctawhatchee and St. Andrews bays	4	7–9	7–8	7.75	.97	.48	75	25
Apalachicola River	11	8–9	8–9	8.55	.54	.16	45	55
Ochlockonee River	5	8–9	8–9	8.40	.58	.26	60	40
Fenholloway River	20	7–9	7–8	7.80	.53	.12	95	5
Suwannee River	19	7–9	7–8	7.84	.50	.12	95	5
M. s. floridanus								
Florida peninsula	73	7–10	8–9	8.55	.60	.07	45	55
Intergrades								
Nassau and St. Marys rivers	10	7–9	7–8	7.70	.68	.22	90	10
Satilla River	20	7–8	8	7.90	.31	.07	100	0
Altamaha River	7	7–9	8	8.00	.53	.20	86	14
Savannah River	11	7–9	8	8.00	.58	.17	91	9
M. s. salmoides								
South Carolina north of Savannah River	77	7–9	7–8	7.91	.51	.06	91	9

TABLE IV

SUBSPECIFIC DIFFERENTIATION AND INTERGRADATION OF *Micropterus salmoides* IN NUMBER OF SCALES ALONG LATERAL LINE

Subspecies and Drainage Basins	Specimens	Total Range	Usual Range	Mean	SD	SE	Percentages	
							58–66	67–76
M. s. salmoides								
Great Lakes and Mississippi River	78	59–69	61–65	63.33	2.12	.24	92	8
Mobile River	15	61–67	61–64	63.27	1.68	.43	93	7
Big Lake, Ala.	22	60–68	63–66	64.32	1.99	.42	91	9
Pensacola Bay	10	58–68	59–65	62.60	3.03	.90	90	10
Intergrades								
Choctawhatchee and St. Andrews bays	5	62–73	67–73	67.80	3.96	1.77	20	80
Apalachicola River	11	64–72	65–70	67.73	2.25	.68	27	73
Ochlockonee River	5	63–76	69–76	70.00	2.40	1.07	20	80
Fenholloway River	20	64–72	65–70	68.15	2.41	.54	25	75
Suwannee River	19	61–73	64–69	66.42	2.92	.67	47	53
M. s. floridanus								
Florida peninsula	74	65–75	69–73	70.42	2.14	.25	4	96
Intergrades								
Nassau and St. Marys rivers	10	58–68	61–67	63.70	2.99	.95	80	20
Satilla River	20	62–68	63–67	65.55	1.91	.43	65	35
Altamaha River	7	64–70	65–70	67.29	2.29	.86	43	57
Savannah River	11	63–71	65–69	67.18	2.27	.68	45	55
M. s. salmoides								
South Carolina north of Savannah River	76	59–69	63–67	64.61	1.93	.22	83	17

TABLE V

SUBSPECIFIC DIFFERENTIATION AND INTERGRADATION OF *Micropterus salmoides* IN NUMBER OF SCALES BELOW LATERAL LINE

Subspecies and Drainage Basins	Specimens	Total Range	Usual Range	Mean	SD	SE	Percentages	
							14–16	17–18
M. s. salmoides								
Great Lakes and Mississippi River	46	14–17	15–17	15.52	.90	.13	85	15
Mobile River	15	14–16	14–16	14.73	.89	.23	100	0
Big Lake, Ala.	22	14–17	14–15	15.14	.81	.17	91	9
Pensacola Bay	10	14–16	14–15	14.80	.79	.25	100	0
Intergrades								
Choctawhatchee and St. Andrews bays	4	16–17	17	16.75	.52	.26	25	75
Apalachicola River	11	15–18	16–18	16.55	.95	.29	55	45
Ochlockonee River	5	15–16	15–16	15.60	.58	.26	100	0
Fenholloway River	20	15–17	16–17	16.10	.64	.14	75	25
Suwannee River	19	14–17	15–16	15.58	.67	.16	95	5
M. s. floridanus								
Florida peninsula	73	16–18	17–18	17.01	.67	.08	22	78
Intergrades								
Nassau and St. Marys rivers	10	15–16	16	15.80	.43	.14	100	0
Satilla River	20	14–17	15–16	15.45	.77	.17	90	10
Altamaha River	7	14–16	15–16	15.29	.76	.29	100	0
Savannah River	11	14–16	16	15.73	.69	.21	100	0
M. s. salmoides								
South Carolina north of Savannah River	76	14–17	15–16	15.36	.74	.08	99	1

TABLE VI

SUBSPECIFIC DIFFERENTIATION AND INTERGRADATION OF *Micropterus salmoides* IN NUMBER OF SCALE ROWS AROUND CAUDAL PEDUNCLE

Subspecies and Drainage Basins	Specimens	Total Range	Usual Range	Mean	SD	SE	Percentages	
							24–28	29–32
M. s. salmoides								
Great Lakes and Mississippi River	37	24–30	26–28	27.22	1.25	.21	95	5
Mobile River	15	24–28	26–28	26.33	1.12	.29	100	0
Big Lake, Ala.	22	24–28	26–27	26.14	.97	.21	100	0
Pensacola Bay	10	25–27	26	26.00	.67	.21	100	0
Intergrades								
Choctawhatchee and St. Andrews bays	5	24–28	26–28	26.80	1.83	.82	100	0
Apalachicola River	11	26–30	26–28	27.64	1.18	.35	91	9
Ochlockonee River	5	27–31	27–30	28.80	1.79	.80	40	60
Fenholloway River	20	25–30	28–29	27.95	1.10	.25	75	25
Suwannee River	19	26–29	26–28	27.37	1.02	.23	95	5
M. s. floridanus								
Florida peninsula	72	27–32	28–31	29.71	1.28	.15	25	75
Intergrades								
Nassau and St. Marys rivers	10	24–29	27–28	27.60	1.36	.43	90	10
Satilla River	20	25–29	26–28	27.45	1.06	.24	90	10
Altamaha River	7	26–28	27–28	27.29	.76	.29	100	0
Savannah River	11	26–29	26–28	27.45	1.05	.32	91	9
M. s. salmoides								
South Carolina north of Savannah River	75	24–29	26–28	27.12	.98	.11	99	1

TABLE VII

SUBSPECIFIC DIFFERENTIATION AND INTERGRADATION OF *Micropterus salmoides:* IN MERISTIC INDEX
This meristic index is the sum of the 5 scale rows detailed in Tables II–VI

Subspecies and Drainage Basins	Specimens	Total Range	Usual Range	Mean	SD	SE	Percentages 113–130	Percentages 131–145
M. s. salmoides								
Great Lakes and Mississippi River	34	121–132	122–128	125.00	2.65	.45	97	3
Mobile River	15	116–130	119–125	122.26	3.33	.86	100	0
Big Lake, Ala.	22	118–128	122–127	124.05	2.62	.56	100	0
Pensacola Bay	9	116–127	118–124	121.78	3.30	1.10	100	0
Intergrades								
Choctawhatchee and St. Andrews bays	4	130–139	130–132	133.00	4.08	2.04	25	75
Apalachicola River	11	125–137	128–136	131.55	3.54	1.07	27	73
Ochlockonee River	5	124–145	124–141	135.00	8.57	3.83	40	60
Fenholloway River	20	125–136	126–134	131.15	3.45	.77	40	60
Suwannee River	19	118–134	126–134	128.68	4.39	1.01	58	42
M. s. floridanus								
Florida peninsula	72	129–145	135–142	137.93	3.53	.42	3	97
Intergrades								
Nassau and St. Marys rivers	10	113–132	125–129	125.90	4.99	3.16	90	10
Satilla River	20	121–132	124–129	126.95	2.73	.61	90	10
Altamaha River	7	124–131	125–131	128.29	2.63	.99	86	14
Savannah River	11	122–134	129–134	129.45	3.67	1.11	64	36
M. s. salmoides								
South Carolina north of Savannah River	75	119–131	122–128	126.39	2.69	.31	97	3

TABLE VIII

SUBSPECIFIC DIFFERENTIATION AND INTERGRADATION OF *Micropterus salmoides*
SUMMARY OF PERCENTAGES OF COUNTS ABOVE SELECTED LINE OF SEPARATION
Data from Tables II–VII

Subspecies and Drainage Basins	Rows on Cheek	Above Lateral Line	Along Lateral Line	Below Lateral Line	Caudal Peduncle	Meristic Index
M. s. salmoides						
Great Lakes and Mississippi River	14	9	8	15	5	3
Mobile River	7	13	7	0	0	0
Big Lake, Ala.	18	0	9	9	0	0
Pensacola Bay	0	0	10	0	0	0
Intergrades						
Choctawhatchee and St. Andrews bays	60	25	80	75	0	75
Apalachicola River	36	55	73	45	9	73
Ochlockonee River	60	40	80	0	60	60
Fenholloway River	35	5	75	25	25	60
Suwannee River	53	5	53	5	5	42
M. s. floridanus						
Florida peninsula	84	55	96	78	75	97
Intergrades						
Nassau and St. Marys rivers	40	10	20	0	10	10
Satilla River	15	0	35	10	10	10
Altamaha River	0	14	57	0	0	14
Savannah River	36	9	55	0	9	36
M. s. salmoides						
South Carolina north of Savannah River	6	9	17	1	1	3

In color pattern (Pl. II; see also Allen, 1946: 27, fig.) *M. s. floridanus* differs somewhat from *M. s. salmoides,* but many individuals cannot be properly identified on this basis alone. In *floridanus* the dark blotch at the base of the caudal fin in young and yearlings is more rounded in front, is much larger, and, commonly, is more intense (with age the spot becomes obscure in both subspecies). The lateral dark stripe is usually broader and darker on the caudal peduncle than in specimens of *salmoides* from the northern states, but individuals from bog-stained waters of the southern coastal plain may have an equally dark and broad stripe, as well as a large basicaudal spot. Anteriorly, the lateral stripe is more disrupted in *floridanus,* forming a series of more or less distinct blotches.

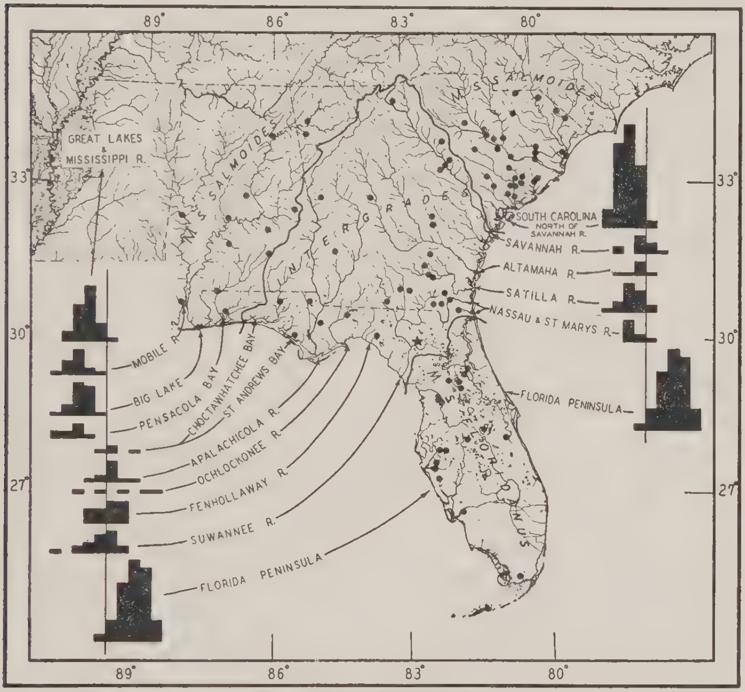
Except for the slightly higher mean value for the number of pectoral rays, *floridanus* appears not to differ appreciably from *salmoides* in fin-ray counts: the dorsal spines number 9 in 5 specimens, 10 in 61, and 11 in 2 (mean, 9.95); dorsal soft rays, 12 in 5, 13 in 58, and 14 in 5 (mean, 13.00); anal spines, 3 in 68; anal soft rays, 10 in 5, 11 in 60, and 12 in 3 (mean, 10.97); pectoral rays 14–14 in 9, 14–15 in 4, 14–14 in 2, 15–15 in 41, 15–16 in 3, 16–15 in 4, and 16–16 in 4 (mean for 134 counts, 14.93). The comparable values given by Hubbs and Bailey (1940: Table IV) apply to *M. s. salmoides.*

Among 57 specimens of *floridanus* examined for this character only 1 specimen has the tongue toothed, and it has only a single small glossohyal tooth.

RANGE.—*M. s. floridanus* is confined to Florida, where it ranges throughout the peninsula northward in the east to the mouth of the St. Johns River and in the west to, but not including, the Suwannee River system. Farther to the north and to the west it intergrades with *M. s. salmoides,* as is indicated in the following section.

SUBSPECIFIC INTERGRADATION

Although throughout most of peninsular Florida *Micropterus salmoides floridanus* is almost invariably separable from typical *M. s. salmoides* by the meristic index, the 2 forms blend in a moderately wide band of intergradation (Map 1 and Tables II–VIII). Physiographic barriers in the form of well-drained soils, which extend from the coast to well inland, limit the area of intergradation. One such barrier occurs between the Pensacola Bay and Choctawhatchee Bay drainages,


89°
86°
83°
80°
33°
30°
27°
GREAT LAKES & MISSISSIPPI R.
M. S. SALMOIDES
M. S. SALMOIDES
INTERGRADES
M. S. FLORIDANUS
SOUTH CAROLINA NORTH OF SAVANNAH R.
SAVANNAH R.
ALTAMAHA R.
SATILLA R.
NASSAU & ST MARYS R.
FLORIDA PENINSULA
MOBILE R.
BIG LAKE
PENSACOLA BAY
CHOCTAWHATCHEE BAY
ST ANDREWS BAY
APALACHICOLA R.
OCHLOCKONEE R.
FENHOLLAWAY R.
SUWANNEE R.
FLORIDA PENINSULA

MAP 1. Florida and adjacent regions, showing the type locality of *Micropterus notius* (star) and the range of *Micropterus salmoides floridanus* and of intergrades between this subspecies and *M. s. salmoides* (circles). Heavy lines separate the ranges of the subspecies from the area of intergradation. Locality records are indicated only for the material used in the present study.

The histograms show for *M. salmoides* the variation in the meristic index by drainage basin or other geographic area; the data are grouped by threes (113–115, 116–118, etc.) and a vertical line indicates the separation between values of 130 to 131. The data from which these histograms were prepared are summarized in Table VII. Map drafted by N. J. Wilimovsky.

and another extends from near the mouth of the Suwannee River north into Georgia and east almost to the St. Johns River (Hobbs, 1942 : Map 2). Gene flow across these areas is probably so slight as to prevent appreciable modification of the characters of the subspecies in their respective ranges. Blending of characters in the area of intergradation may be seen by comparing the ranges, the means, and the percentages of specimens below and above the selected lines of separation. With some exceptions and irregularities for certain counts at certain localities, all the scale counts for series across this belt are intermediate, often about median in average. Thus, *M. s. floridanus* is genetically connected with the main body of *M. s. salmoides,* presumably as the result of gene flow.

Toward the north, that is toward the nomenclatorially typical *M. s. salmoides* of South Carolina, the intergradation is not so clear nor so regular. Populations from the Nassau and St. Marys river systems near the Florida–Georgia border to the Savannah River system of Georgia and South Carolina usually approach *M. s. salmoides* in counts but in some respects show transition: the sample from the Nassau and St. Marys river systems is definitely intermediate in the count of scale rows on the cheek; series from the Satilla and Altamaha river systems are interjacent in the count of scales along the lateral line; the series from the Savannah system is intermediate in the counts for the scales on the cheek and on the lateral line and in the meristic index. Oddly, the three other river-system categories, particularly the two more southern ones, are very close to topotypical *M. s. salmoides* in the meristic index. Though some of their counts are higher than those for South Carolina specimens from north of the Savannah River, other counts are comparatively low. The break between *M. s. floridanus* in the St. Johns system and the intergrades in the Nassau and St. Marys systems (Map 1) is abrupt. This fact, as well as the imperfect and irregular intergradation, suggest to us the possibility that a natural orderly situation has been complicated by the extensive stocking of northern *salmoides.* Much of the collecting in the area where more regular intergradation might be expected has been along U. S. Highway No. 1, which may also have served as the route by which the northern stock was introduced, to modify the genetic composition of the natural populations. An alternative explanation for the abrupt change in characters involves the possibility of the extirpation of intergrading populations in this area during a period of marginal submergence in late Pleistocene, when much of the eastern margin of the peninsula was reduced to a coastal archipelago (Carr, 1940: 6). If this happened, the evidence indicates that subsequent reinvasion of the area north of the St. Johns River was largely from the north.

According to our interpretation the area of intergradation (Map 1) divides the range of *M. s. salmoides* into 2 parts, respectively, east and west of the Appalachian Mountains. It may be assumed that formerly this subspecies was continuously distributed along the coastal plain from South Carolina to Alabama and Mississippi. *M. s. floridanus* probably differentiated on the Florida Peninsula under conditions of partial or complete isolation, most likely during one of the Pleistocene interglacial periods. (See description and maps in Cooke, 1939: 33–61, and Cooke, 1945: 273–311.) Such isolation might have occurred during the Coharie, the Sunderland, or the Wicomico stage, when the land was reduced to islands, with consequent reduction of the fresh water of the area, or it may have taken place during the Penholaway, the Talbot, or the Pamlico stage, when the peninsula existed but was more nearly separated from the mainland than it is at present.

Subsequent to differentiation, when confronted with less effective barriers to migration, *M. s. floridanus* may be assumed to have spread to the north and to the northwest, where it met *M. s. salmoides.* Since the differentiation of *floridanus* from *salmoides* had not reached the specific level, the meeting of the subspecies resulted in amalgamation of the forms in what is now the area of intergradation (Map 1). Thus, according to this hypothesis, intergradation between these subspecies is the result of fusion in an area accessible to both races following partial or complete disappearance of the isolating barrier.

THE FLORIDA LARGEMOUTH BASS AS AN ELEMENT IN THE ENDEMIC PENINSULAR FAUNA

The recognition of *Micropterus salmoides floridanus* adds 1 more element to the list of endemic Florida peninsular fishes. The peninsula has long been noted for endemism of various groups of organisms, such as the ferns (St. John, 1936), crayfishes (Hobbs, 1942), and amphibians and reptiles (Carr, 1940), but very little consideration has been given to the peninsular endemism of the fresh-water and brackish-water fishes. We therefore append a list of fishes that are entirely endemic or chiefly characteristic of the Florida peninsula.

LIST OF FISHES ENDEMIC TO, OR CHIEFLY CHARACTERISTIC OF, THE FLORIDA PENINSULA

(Endemic elements in boldface type)[6]

A. Forms which are strictly endemic to Florida:
- *Signalosa petenensis* **vanhyningi** Weed
- **Chriopeops goodei** (Jordan)
- *Fundulus* **seminolis** Girard
- *Fundulus confluentus* **confluentus** Goode and Bean
- *Floridichthys carpio* **carpio** (Günther)
- **Jordanella floridae** Goode and Bean
- *Cyprinodon* **hubbsi** Carr
- *Micropterus* **notius** Bailey and Hubbs
- *Micropterus salmoides* **floridanus** (LeSueur)

B. Forms which are typically Floridian but which occur also in the Okefenokee Swamp area in southeastern Georgia:
- **Leptolucania ommata** (Jordan)
- *Mesogonistius chaetodon* **elizabethae** Bailey

C. Forms which are characteristically Floridian but which range well to the north along the Atlantic coastal plain (but not beyond North Carolina):
- *Lepisosteus* **platyrhincus** DeKay
- *Notropis* **hypselopterus** (Günther)
- *Fundulus dispar* **lineolatus** (Agassiz)
- *Labidesthes sicculus* **vanhyningi** Bean and Reid
- *Lepomis punctatus* **punctatus** (Valenciennes)
- *Elassoma* **evergladei** Jordan
- *Hololepis* **barratti** (Holbrook)

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[6] In addition to the forms named, we have unpublished evidence that at least 5 more forms may eventually be added to the list.

SUMMARY AND CONCLUSIONS

The black bass genus *Micropterus,* long thought to comprise only 2 species, is now shown to encompass 5 full species and a total of 10 forms, subspecies included. In addition, the probable existence of 2 more forms, 1 perhaps a full species, is suggested. The forms that we now add are peripheral in distribution and thus add weight to the theory that most differentiation occurs at the margins of ranges.

Micropterus notius, new species, is known from a single spring in northern Florida. It may be a relict form, as it appears to be the most generalized species of *Micropterus.* Although it closely resembles *Micropterus* (*Huro*) *salmoides* in some respects, this distinct species is referred to the subgenus *Micropterus.* The possibility of its being of hybrid origin is discounted. Hybridization is unknown between *Micropterus* and *Huro,* which are now treated as subgenera. Even interspecific hybrids in the same subgenus are very rare. One additional example, a hybrid between *M. dolomieu* and *M. punctulatus,* is described.

Micropterus species, from the Chipola River in western Florida, is described on the basis of a single specimen, but is left unnamed. It may be either a full species, a subspecies, or a variant of *M. punctulatus* or of *M. coosae.*

Micropterus salmoides floridanus (LeSueur) is recognized as the largemouth bass of peninsular Florida. It is characterized by its small scales, large size, and rather distinctive coloration. Reports of *M. dolomieu* from Florida, including the record-sized "smallmouths," appear to have been based on this subspecies of *M. salmoides. M. s. floridanus* intergrades geographically with *M. s. salmoides.* The intergradation may have resulted from the amalgamation of the subspecies in a region accessible to both, following the disappearance of an isolating barrier. There are indications of the existence of additional subspecies of *M. salmoides,* including a southwestern form with a high incidence of glossohyal teeth.

The 3 forms shift the center of known abundance of the kinds of black basses to the southeast. In addition, *M. punctulatus* is recorded from Florida.

Each of these 3 forms from Florida (*M. notius, M.* species, and *M. s. floridanus*) is an addition to a region of endemism. Northern Florida, western Florida, and peninsular Florida are centers of endemism for fishes, as well as for other organisms.

Bartramiolus Fowler is shown to be a synonym of *Ambloplites,* since its designated genotype, *Ambloplites ariommus,* intergrades in eastern Arkansas and southeastern Missouri with *Ambloplites rupestris rupestris.*

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PLATE I

Fig. 1. *Micropterus notius,* new species, from the holotype, a fingerling, 68 mm. long.

Fig. 2. *Micropterus notius,* new species, from an adult paratype, 219 mm. long (U.M.M.Z., No. 134629).

Photographs by F. W. Ouradnik.

PLATE I

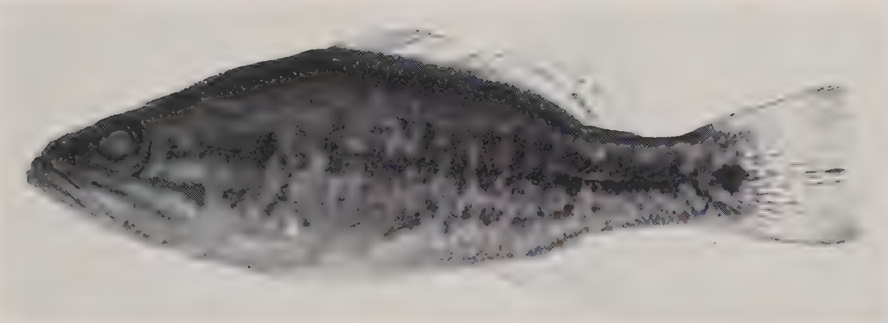

FIG. 1

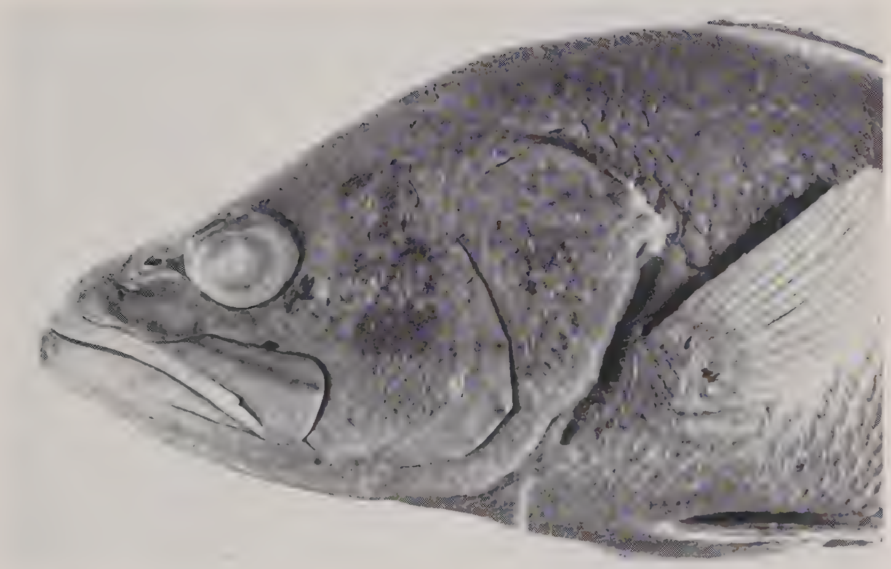

FIG. 2

Contribution No. 416

THE DIATOMS COLLECTED BY THE U. S. S. CACOPAN IN THE ANTARCTIC IN 1947[1]

By

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For investigation of the Diatomaceae, a series of water samples was collected from the U. S. S. Cacopan by filling a citrate bottle either with surface water obtained with a bucket or with water obtained from various depths with Nansen bottles. The positions at which samples were collected in the Antarctic are plotted on Fig. 1. Of the main previous Antarctic Expeditions (Challenger, Deutscher Sudpolar, Valdivia and Discovery) only the Challenger collected much diatom material on the Pacific and Indian Ocean side of the Antarctic continent. Five stations were occupied by the Challenger in this area, but most of the diatom material obtained was from bottom sediments. The species of diatoms found at each station by the Cacopan are listed in Table I with notations indicating the relative abundance of diatoms at each station. Further information on each station (Depth, Temperature, etc.) is given in the appendix.

Identification and estimation of abundance were carried out on semi-permanent strewn plankton mounts. The diatoms were washed six times in distilled water, allowed to settle for 24 hours between washings, and the supernatant water drawn off by means of a fine pipette attached to a vacuum pump. After the final washing a few drops of the sediment were placed on a slide, gently warmed until dry, and a permanent mount prepared. For a critical examination of the species a mountant with a high refractive index is necessary. For this purpose Hyrax (a synthetic resin with a refractive index of 1.71) was used. These preparations give excellent results and last for many months.

According to the hydrographic data (Pritchard and LaFond, MS.), the Antarctic Convergence is not sharply defined in the region from which most of the diatom samples were taken, but lies somewhere between Lat. 59° S. and 63° S. The surface water temperature difference—about 6° C.—between stations 42 and 44 is an indication that the Convergence had been crossed, and all higher numbered stations were therefore situated to the north of the Convergence. It appears

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[1] Contributions from the Scripps Institution of Oceanography, New Series, No. 416.

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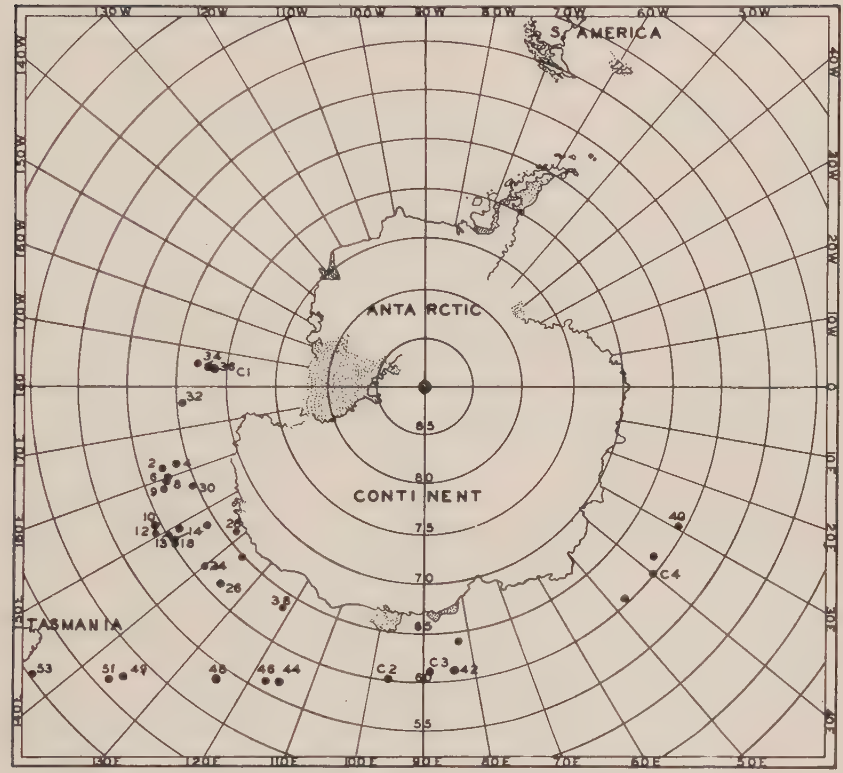
S. AMERICA
ANTARCTIC
CONTINENT
TASMANIA
130W
120W
110W
100W
90W
80W
70W
60W
50W
140W
150W
160W
170W
180
170E
160E
150E
140E
40W
30W
20W
10W
0
10E
20E
30E
40E
130E
120E
110E
100E
90E
80E
70E
60E
50E
85
80
75
70
65
60
55
34
36
C1
32
2
4
6
8
9
30
10
12
13
14
18
20
24
26
38
53
51
49
48
46
44
C2
C3
42
40
C4

Figure 1. Chart of Antarctic stations.

from Table I that the Antarctic Circumpolar surface water south of the Convergence supports an extremely rich phytoplankton population compared with the striking paucity of phytoplankton in the surface waters to the north of the Convergence. The phytoplankton wealth of the Antarctic waters has frequently been commented upon before (Hendey, 1937; Hart, 1934). Hart has suggested that the diminished population in the subtropical and tropical regions is a result of the almost complete lack of nutrient salts in the surface waters of these regions, while in the polar regions nutrients cannot be regarded as a limiting factor at any time, since the content never falls below a minimum of about 0.9 μg.-at. PO_4 per liter, which is well above diatom needs. Hart considers that the high nutrient content is due to the fact that the spring break-up of the ice packs releases a supply that is never exhausted. Another cause of this nutrient surplus, and probably the main cause, is the marked vertical mixing of the Antarctic waters

76	74	72	70	67	65	63	61	59	55	53	51	49	48	46	44	42	40	38	36	34	32	30	28	26	24	18	14	13	12	10	9	8	6	4	2	Station Number
VR	VR	VR	O	O	O	VR	VR	O	VR	O	VR	VR	VR	VR	R	A	C	VA	C	C	R	C	R	A	C	C	A	A	C	A	VA	C	C	C	C	Relative Diatom Abundance
																														+						Actinocyclus bifrons Karsten, 1905, p. 92.
																		+																		Actinocyclus janus Karsten, 1905, p. 92.
																+																				Amphora peragallorum van Heurck, 1909, p. 7.
																													+							Asteromphalus brookei Bailey, 1856, p. 2.
																			+							+	+									Asteromphalus elegans Greville, 1859, p. 161.
																+								+		+		+								Asteromphalus heptactis (Brébisson) Ralfs ex Pritchard, 1861, p. 838.
																+									+	+	+		+	+					+	Asteromphalus parvulus Karsten, 1905, p. 90.
															+									+	+										+	Asteromphalus roperianus Ralfs ex Pritchard, 1861, p. 838.
																+																				Chaetoceros chunii Karsten, 1905, p. 117.
																+	+	+	+	+		+	+			+	+	+	+	+		+	+	+		Chaetoceros criophilum Castracane, 1886, p. 78.
																+	+	+	+	+	+	+			+	+	+	+	+	+	+	+		+		Chaetoceros dichaeta Ehrenberg, 1844, p. 200
						?																													+	Chaetoceros didymum Ehrenberg, 1845, p. 75.
																											+									Chaetoceros neglectum Karsten, 1905, p. 119
																							+										+			Chaetoceros pelagicum Cleve, 1873, p. 11.
															+	+	+	+		+		+		+	+		+	+	+	+	+					Chaetoceros peruvianum Brightwell, 1856, p. 107.
																+													+		+					Charcotia bifrons (Castracane) M. Peragallo, 1921, p. 78.
																+	+	+				+	+	+		+	+	+	+	+	+	+	+	+		Corethron criophilum Castracane, 1886, p. 85.
																								+												Coscinodiscus australis Karsten, 1905, p. 79.
																										+										Coscinodiscus excentricus Ehrenberg, 1840, p. 146.
																																+				Coscinodiscus gracilis Karsten, 1905, p. 78.
																										+	+			+		+	+	+		Coscinodiscus lentiginosus Janisch, In Schmidt, 1878, p. 58.
																								+		+										Coscinodiscus lineatus Ehrenberg, 1839, p. 129.
																								+												Coscinodiscus minimus Karsten, 1905, p. 78.
																	+							+	+	+									+	Coscinodiscus simbirskianus Grunow, 1884, p. 81.
+																					+											+			+	Cocconeis sp.
														+	+	+		+						+		+	+	+		+	+					Dactyliosolen antarcticus Castracane, 1886, p. 75.
																+		+						+		+	+	+					+	+	+	Eucampia balaustium Castracane, 1886, p. 97.

76	74	72	70	67	65	63	61	59	55	53	51	49	48	46	44	42	40	38	36	34	32	30	28	26	24	18	14	13	12	10	9	8	6	4	2	
VR	VR	VR	O	O	O	VR	VR	O	VR	O	VR	VR	VR	VR	R	A	C	VA	C	C	R	C	R	A	C	C	A	A	C	A	VA	C	C	C	C	
																												+								Eucampia cornuta (Cleve) Grunow ex van Heurck, 1880-5, pl. 95b, f. 5.
																+		+								+					+	+			+	Fragilaria sp.
												+		+	+	+		+	+	+	+			+	+	+		+	+	+	+	+		+	+	Fragilariopsis antarctica (Castracane) Hustedt in Schmidt, 1913, pl. 299, f 9-14
		+							+					+	+	+		+	+	+	+			+	+	+	+	+	+	+	+	+		+	+	Fragilariopsis antarctica f. bouvet Karsten, 1905, p. 123.
														+				+	+																	Grammatophora marina (Lyngbye) Kützing, 1844, p. 128.
																		+							+		+			+				+		Guinardia flaccida (Castracane) H. Peragallo, 1892, p. 107.
																		+								+										Navicula trompii var. major Heiden & Kolbe, 1928, p. 625.
																+		+			+							+	+			+		+	+	Nitzschia closterium (Ehrenberg) W. Smith, 1853, p. 42.
	+						+							+	+	+	+	+		+				+	+	+	+	+	+	+	+	+	+	+	+	Nitzschia seriata Cleve, 1883, p. 478.
																														+						Pinnularia lanceolata Heiden & Kolbe 1928, p. 598.
														+												+				+						Pleurosigma directum Grunow, 1880, p. 53.
	+												+															+		+						Rhizosolenia alata Brightwell, 1858, p. 96.
																+														+						Rhizosolenia alata f. indica (Peragallo) Hustedt, 1929, p. 602.
						+					+				+	+	+	+							+	+	+	+	+	+	+	+	+	+		Rhizosolenia alata f. inermis (Castracane) Hustedt, 1929, p. 602.
																		+														+				Rhizosolenia antarctica Karsten, 1905, p. 95.
																+																				Rhizosolenia bidens Karsten, 1905, p. 98.
																								+							+					Rhizosolenia delicatula Cleve, 1900, p. 28.
																+								+		+	+	+	+	+	+		+			Rhizosolenia hebetata f. semispina (Hensen) Gran, 1905, p. 55.
															+							+			+											Rhizosolenia styliformis v. longispina Hustedt in Schmidt, 1914, pl. 316, f 3-7,12
																								+												Schimperiella antarctica Karsten, 1905, p. 88.
																+	+	+	+		+					+	+	+	+	+		+	+	+	+	Synedra pelagica Hendy, 1937, p. 335.
																		+						+		+					+					Thalassiosira antarctica Comber, 1896, p. 491.
																												+				+		+		Thalassiosira decipiens (Grunow ex van Heurck) Jörgensen, 1905, p. 96.
																+		+						+	+	+		+	+	+	+	+				Thalassiothrix longissima v. antarctica
															+			+						+		+			+		+		+		+	Tropidoneis antarctica (Grunow) Cleve, 1894, p. 24.
																				+																Tropidoneis glacialis v. constricta Heiden & Kolbe, 1928, p. 656.
																													+							Rhizosolenia styliformis Brightwell, 1858, p. 95.

and weak thermal stratification resulting in the ascent of nutrient-rich deep water (Sverdrup, Johnson and Fleming, 1942: 620). This nutrient surplus was also indicated by the CACOPAN collection.

Four hydrographic stations, shown in Fig. 1, were occupied in the polar waters. The vertical thermal structure at these four stations (Fig. 2) reveals a marked seasonal thermocline with a drop in temperature of nearly 5° C. at depths of 20–40 meters.[2] The presence of this stratification shows that the surface waters there have already spent some time as such. A certain degree of vertical stability, as is indicated here, has been considered necessary for maximum diatom production, otherwise many of the diatoms are carried down below the euphotic zone (Gran and Braarud, in Sverdrup, et al., 1942: 789). Thus, although data on the actual nutrient content of the water are lacking, the high diatom population in the euphotic zone above the thermocline (in surface waters which are "aged") is strong evidence that there is still a sufficiency of nutrients for good phytoplankton production.

On crossing the Antarctic Convergence to the north, a pronounced drop in phytoplankton population is noted. The thermal structure in this region (Fig. 3) can be taken as an indication that vertical movement between the waters of the euphotic zone above the thermocline and the lower layers is much reduced, and thus the replenishment of nutrients is slow. The paucity of diatom cells here may indicate that the vernal bloom is over and that the surface water nutrients are depleted. The appearance of a summer form such as *Rhizosolenia hebetata* f. *semispina* and the absence of the primitive resting stage of *Rhizosolenia hebetata* are indications that the population is a summer one.

The species concentration found at each depth at the hydrographic stations is as follows:

Station C1		*Station C2*		*Station C3*		*Station C4*	
Depth (feet)	*No. of Species*	*Depth (feet)*	*No. of Species*	*Depth (feet)*	*No. of Species*	*Depth (feet)*	*No. of Species*
0	3	0	1	0	8	0	3
50	1	50	7	50	9	50	8
100	1	100	7	100	6	100	8
200	1	200	1	200	5	200	8
300	0	300	2	300	1	300	0
500	0	500	1	600	0	500	0
900	0	900	1			650	0

As each species was usually represented by only one or two frustules, the number of species can be taken as an indication of diatom concentration. The depths at which a Secchi disc could be seen at these four stations were as follows: Sta. C1, 90 ft.; Sta. C2, 55 ft.; Sta. C3, 41 ft.; Sta. C4, 68 ft. Diatoms flourish best in somewhat subdued

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[2] There is no winter thermocline in Antarctic waters (Sverdrup, et al., 1942: 609).

Table I. Species and Abundance of Diatoms. VA—very abundant, A—abundant, C—common, R—rare, VR—very rare, O—None detected.

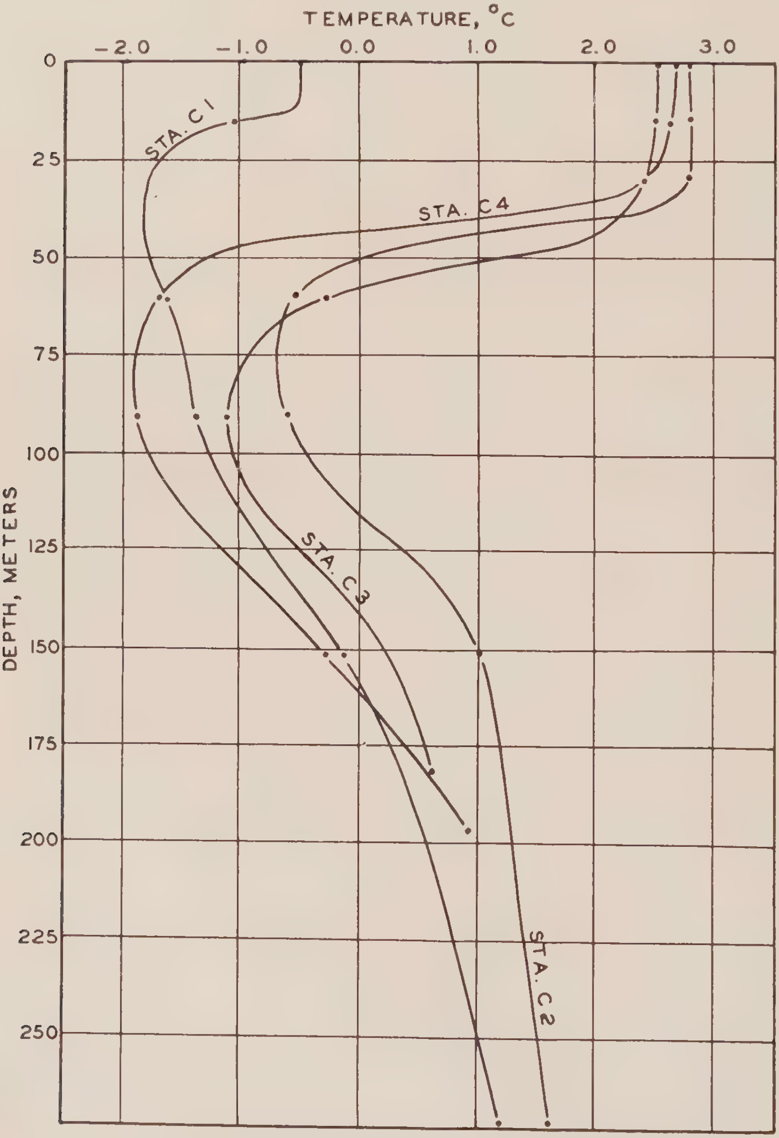

Figure 2. Vertical thermal structure at hydrographic stations.

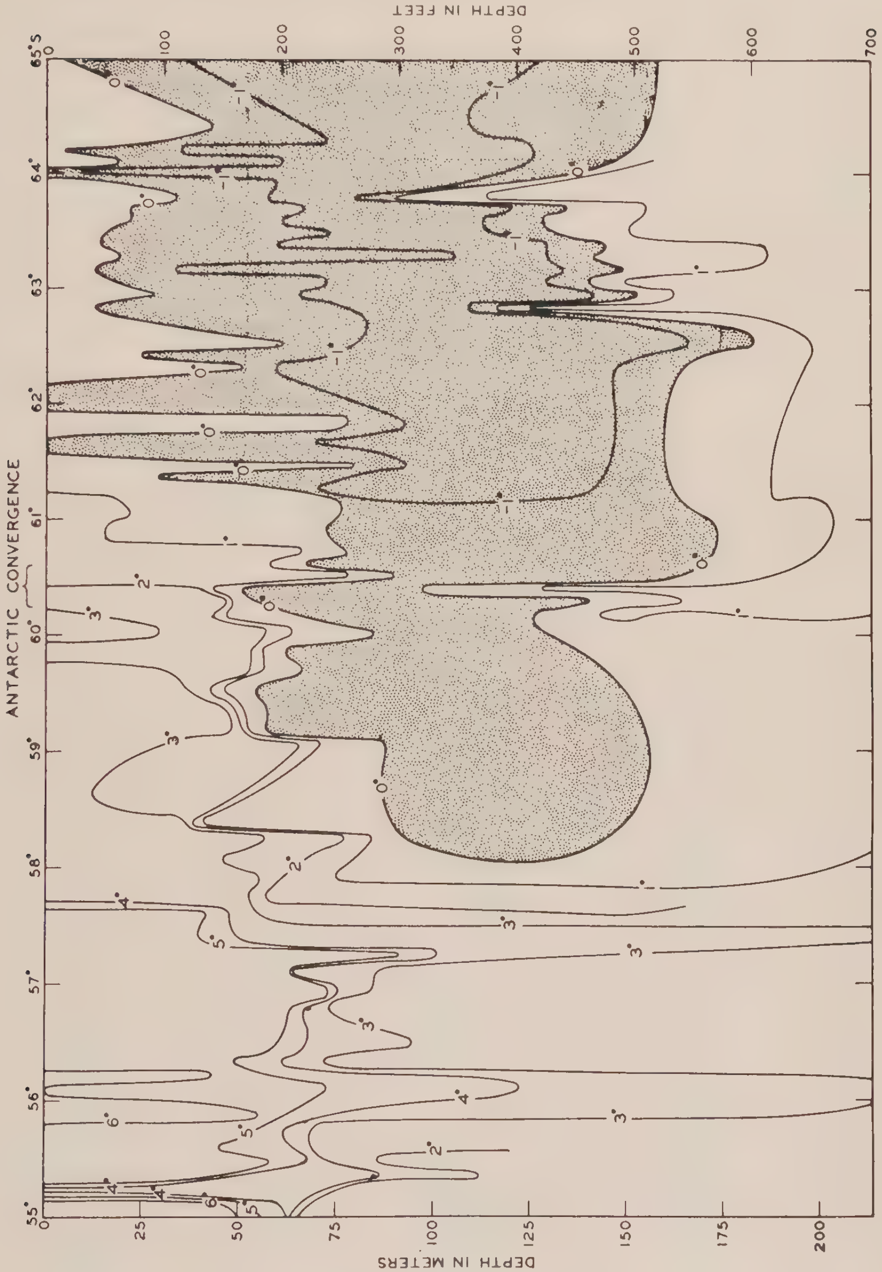

Figure 3. Vertical temperature sections across Antarctic convergence.

light and hence there is usually a subsurface diatom maximum. Schimper (Karsten, 1905) found diatom maxima at 40–80 m. in the Antarctic. Sverdrup, Johnson and Fleming (1942: 781) consider that this can be attributed only to sinking, since photosynthesis cannot occur in these latitudes below 50 m. Although there is some slight indication of a subsurface diatom maximum in the above data, it is not conclusive. Indeed, it is doubtful whether sunlight is ever sufficiently intense at these latitudes to become lethal to diatoms or inhibitory to their growth even at the extreme surface. The only conclusions that can be drawn from the present data are (a) that the euphotic and disphotic zones at these stations are extremely shallow, and (b) that probably the lower limit of the disphotic zone is about 200 ft.

ACKNOWLEDGMENTS

I would like to thank Robert Dietz and H. Mann of the Navy Electronics Laboratory, San Diego, who collected the material for this investigation. I am also indebted to E. C. La Fond of N. E. L. for the use of Fig. 3, and for obtaining permission from the Navy to publish this material.

APPENDIX

SURFACE SAMPLES

Station	*Latitude (S)*	*Longitude*	*Temp. (° C.)*	*Date*
2	62° 2′	162° 3′ E.	−0.8	12/28/46
4	62° 5′	162° 0′ E.	1.0	12/29/46
6	62° 2′	159° 2′ E.	0.7	12/30/46
8	61° 8′	158° 2′ E.	1.8	12/30/46
9	61° 0′	156° 2′ E.	2.0	12/30/46
10	59° 3′	152° 0′ E.	1.9	12/31/46
12	59° 2′	150° 4′ E.	1.5	1/ 1/47
13	59° 5′	148° 8′ E.	1.0	1/ 2/47
14	60° 0′	150° 6′ E.	1.6	1/ 3/47
18	59° 9′	148° 8′ E.	1.3	1/ 5/47
24	61° 0′	140° 0′ E.	2.4	1/18/47
26	61° 0′	137° 3′ E.	1.9	1/20/47
28	65° 7′	141° 6′ E.	−0.4	1/22/47
30	64° 5′	156° 0′ E.	0.8	1/23/47
32	65° 5′	176° 1′ E.	2.1	1/25/47
34	66° 9′	173° 8′ W.	1.6	1/27/47
36	68° 1′	174° 7′ W.	−0.2	1/28/47
38	63° 5′	121° 8′ E.	1.0	2/ 7/47
40	60° 7′	29° 7′ E.	3.0	2/21/47
42	63° 9′	82° 3′ E.	−1.4	3/ 2/47
44	56° 6′	115° 7′ E.	4.6	3/ 6/47
46	55° 9′	117° 6′ E.	1.6	3/ 6/47
48	53° 4′	124° 7′ E.	5.7	3/ 7/47
49	47° 3′	135° 6′ E.	9.0	3/ 8/47
51	46° 1′	136° 5′ E.	10.9	3/ 9/47
53	40° 2′	143° 1′ E.	17.0	3/11/47
55	39° 5′	144° 2′ E.	18.1	3/11/47
59	32° 1′	165° 0′ E.	21.7	3/22/47

APPENDIX

SURFACE SAMPLES

Station	*Latitude (S)*	*Longitude*	*Temp. (° C.)*	*Date*
61	29° 9′	170° 0′ E.	24.0	3/23/47
63	26° 3′	175° 6′ W.	24.3	3/24/47
65	22° 6′	179° 7′ W.	27.4	3/24/47
67	18° 4′	174° 9′ W.	29.0	3/25/47
70	14° 2′	170° 3′ W.	30.7	3/26/47
72	09° 9′	165° 9′ W.	30.0	3/27/47
74	03° 5′	159° 5′ W.	27.6	3/29/47
76	01° 6′ N.	154° 9′ W.	27.6	3/30/47
HYDROGRAPHIC STATIONS				
C1:	68° 43′ S.	174° 55′ W.	−0.5	1/30/47
C2:	59° 55′ S.	96° 45′ E.	2.8	2/11/47
C3:	60° 55′ S.	88° 55′ E.	2.6	2/13/47
C4:	59° 57′ S.	40° 30′ E.	2.5	2/19/47

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Contribution No. 417

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Vol. 84, No. 2, March, 1949

DIVERGENT METHODS OF DEVELOPMENT IN MORPHOLOGICALLY SIMILAR SPECIES OF PROSOBRANCH GASTROPODS

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TEN FIGURES

Among the calyptraeid gastropods belonging to the genus *Crepidula* on the coast of southern California, there are 6 species which may be considered as representing three contrasting pairs. Some individuals belonging to each of the two members of each of these pairs are morphologically similar but differ in the type of eggs that they produce as well as in their mode of development. These three pairs of species are (1) *Crepidula nivea* Adams and *C. williamsi* Coe; (2) *C. arenata* Broderip and *C. adunca* Sowerby; (3) *C. onyx* Sowerby and *C. norrisiarum* (Williamson). In each of these pairs the species first mentioned produces small eggs, with relatively little yolk, and these develop into free-swimming pelagic veliger larvae. The other member of the pair forms much larger eggs which have sufficient yolk to enable them to complete development to the adult form while remaining within the egg capsules beneath the parent's foot. Representatives of all these 6 species may occasionally be found in the same tidepool.

All species of *Crepidula* are notoriously variable in size at sexual maturity, as well as in shape of shell, depending on the habitat. Since the shell covers only the dorsal surface of the body, both size and shape must conform to the area of the substrate to which the animal is attached. Otherwise, the foot and ventral surface would be exposed to the attacks of enemies. In some species the pigmentaion and texture of the shells are also variable. As a consequence, there is much confusion in the nomenclature.

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[1] Contributions from the Scripps Institution of Oceanography, New Series, no. 417.

The young *Crepidula* can move about freely but later becomes sedentary and permanently attached to some solid object, usually on reaching the female phase. When the space available for growth is unusually limited, as it is when the *Crepidula* is attached to the inside or outside of a small gastropod shell, the body can attain only a small fraction of the normal size. Even in these dwarfs each organ of the body remains of normal proportions.

In his now classic studies on the embryology of *Crepidula*, Conklin (1897, 1898) reported that in *C. plana* both the cell size of the somatic tissues and the size of the eggs produced are the same in dwarfs as they are in the largest individuals. The size of the body is dependent on the numbers of the costituent cells, rather than on the size. And, correspondingly, the number of eggs produced at each ovulation is roughly proportional to the size of the body, although the size of the eggs remains constant. The number of eggs in a cluster may be three times as great in a large as in a dwarf individual. Coe ('42) has shown that young of dwarf individuals when suitably cultured may reach a size of more than 20 times the volume of the larger parent.

Conklin (1897) found that each of the 4 species of *Crepidula* which he studied was characterized not only by the morphological features of the body and shell, but also by the size of eggs produced and the mode of larval development. *C. fornicata* Lamarck deposits 8000 to 13,000 or more small ova at each ovulation and *C. plana* Say 3000 to 9000. The eggs of both these species develop into pelagic veligers wich have a free-swimming period of two to three weeks before settling to the bottom and transforming to the adult form. *C. aduca* Sowerby and *C. glauca (convexa)* Say, on the other hand, produce a relatively small number, 180 to 220, of much larger ova which are provided with sufficient yolk to enable them to complete development to the adult form while remaining within the egg capsules. The egg of *C. adunca* is approximately 27 times as large as that of *C. plana* but only about one-fiftieth as many eggs are produced at each ovulation. In all the species the volume of eggs laid is roughly proportional to the volume of the adult. The average adult individual of *C. fornicata* is about 20 times the size of that of *C. glauca* and produces 60 times as many eggs but the relative volumes of the body and eggs at each ovulation remains about 15–1.

Young individuals of any of these species may be cultured to the adult condition by allowing them to attach themselves to the inside walls of screened glass jars which are then immersed in the sea for a few months. Mating occurs normally and since the egg capsules are attached to the glass, the larval development during the period of incubation is clearly visible. The following account shows that the type of egg and mode of development may sometimes be more reliable criteria of the species than the characteristics of the shell alone.

It should be recalled in this connection that all species of *Crepidula,* insofar as known, are typically protandric, each individual usually experiencing a functional male phase when young and later changing through a transition period to the female phase. In most species the completeness of development and duration of the male phase is influenced by association with an individual in the female phase. Furthermore, either of these sexual phases may be more or less completely aborted by unfavorable conditions. In some species this is particularly true of the male phase by abnormal temperature or by lack of either suitable nutrition or association with larger individuals (Gould, '17, '17a, '19, '47; Coe, '36, '38, '38a, '48, '48a).

Individuals in the juvenile and early male phases are usually motile but become sedentary and permanently attached to the substrate on reaching the female phase. In all species the eggs are deposited in thin transparent capsules secreted by the oviduct and attached to the substrate beneath the parent's foot.

The propodium thus acts as a brood pouch in which the eggs undergo larval development for two to three weeks or more. During this time the larvae of the species with small eggs have developed into free-swimming veligers which are then liberated into the water (fig. 1, *a, b*). The larvae of species with large eggs, on the contrary, are provided with sufficient yolk to enable them to complete their development to the adult form while remaining within the capsule. During this period of usually 4–7 weeks they pass through a highly modified veliger stage (fig. 1, *c*).

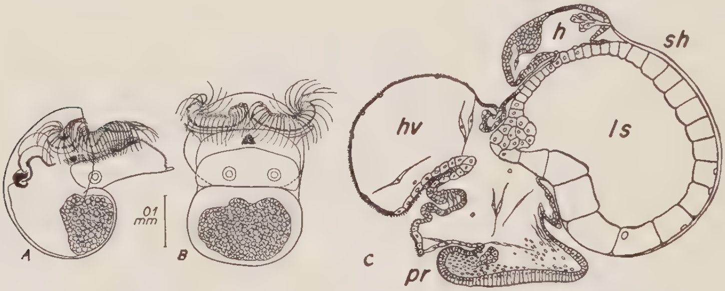

Fig. 1 A, B, pelagic veliger larva of *Crepidula fornicata*. A, from the right, and B, from the ventral side. (From Thorson, '46.) C, non-pelagic larva of *C. adunca; h,* hemocoele; *hv,* head vesicle; *ls,* larval stomach; *pr,* anterior portion of foot; *sh, shell.* (After Moritz, '39.)

1. *Crepidula nivea and C. williamsi*

The young of these two species are easily identified but the adults often appear to be indistinguishable morphologically with the exception of the reproductive organs in the female phase. *C. williamsi* Coe ('47) however produces eggs which are about three times the diameter, or 27 times the volume, of those of the companion species. The former complete their development to the adult condition within the egg capsules, while *C. nivea,* with small eggs, has typical veliger larvae which leave the egg capsules in this condition to swim about as pelagic larvae for a period of presumably several weeks before completing their metamorphosis to the adult condition (fig. 1).

One or both of the two forms under consideration have been generally known as *Crepidula nummaria* Gould but they recently have been shown by Smith ('46) to represent *C. nivea* C. B. Adams. Both forms are most commonly found as occupants of dead gastropod shells, often inhabited also by hermit crabs, but they also occur attached to the under sides of rocks and to other solid objects. As in other species of the genus, the size of the body and shape of the shell is strictly limited to the space available for growth. Consequently only dwarf individuals, commonly less than 20 mm in length are found in small shells, such as those of species of *Tegula*, while individuals living in the shells of large univalves or attached to other solid objects with large surfaces may reach a much larger size (fig. 2). It has been proved experimentally (Coe, '42) that the recently hatched young of the slender,

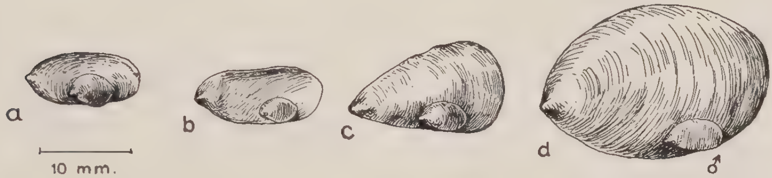

Fig. 2 *Crepidula nivea;* a, b, mature female-phase individuals, dwarf form, with mated males, living in small univalve shells; c, d, same when living on substrate which allows unlimited space for growth.

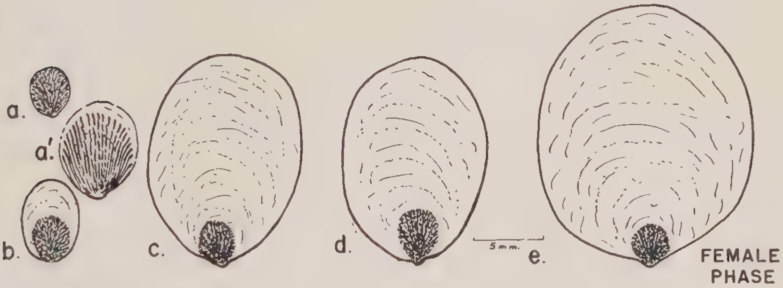

Fig. 3 *Crepidula williamsi.* Growth on an unrestricted surface; a, b, immature and early male phases; c, d, e, mated male, transition and female phases, respectively.

dwarf form of either species may, under suitable conditions, develop into a broadly oval form as much as 20 times the size of the larger parent.

The recently hatched young of *C. williamsi* are brightly spotted with reddish brown pigment. This pigment continues to be produced until the shell has reached a length of 2–4 mm, but in the form of radiating lines rather than as separate spots (fig. 3). Pigment formation usually ceases abruptly at the beginning of the male phase, when the shell is only 2–4 mm long and thereafter only white, porcelaneous shell is usually produced. In exceptional cases, however, scattered pigment spots or traces of interrupted radiating lines may extend over much of the adult shell. In a protected habitat the juvenile pigmentation may be retained at the apex of the shell in mature individuals but when the *Crepidula* inhabits the interior of a snail shell which is occupied also by a hermit crab, the abrasive action due to the crab's movements wears off the apical pigment, leaving only the white underlying shell (fig. 4).

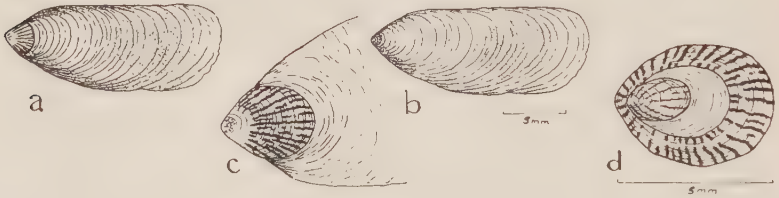

Fig. 4 *Crepidula williamsi.* Shape assumed in shells of Tegula; a, juvenile pigmentation retained; b, juvenile pigmentation eroded; c, pigmentation eroded only at apex; d, alternating periods of pigment deposition on shell.

A number of observers have mentioned more or less pigmentation on the shells of supposedly *C. nivea* without realizing that such markings are indicative of a different species. Young, as well as adults, of *C. nivea* are almost invariably devoid of dark pigment. In the female phase the two species can usually be distinguished externally by the color of the ovaries, since the large ova with much yolk are deep orange, while the small ova of *C. nivea* are pale yellow. Otherwise, if the apical pigment is missing, the writer knows of no way of differentiating the shells of the two species after the animals have been removed. Young of both species are sometimes found side by side in the same snail shell but in small shells, like those of *Tegula*, it is unusual for more than one individual to reach maturity. In such situations *C. nivea* is usually more than twice as abundant as *C. williamsi* and of larger average size when adult. When the young of both species are cultured in the same jar, those of *C. nivea* increase in size much more rapidly and deposit their egg clusters at an earlier age than those of *C. williamsi.*

In each species the male phase usually becomes functional when the animal has reached a length of 4–6 mm and may be retained until the length is 14 mm or more. More frequently the sexual transformation to the female phase occurs at a length of 7–8 mm. In solitary or experimentally isolated individuals the male phase may be more or less completely aborted, as Gould ('17) and Coe ('48a) have reported for *C. plana.* The functional males usually mate with individuals of their own species, not only in nature but also when females of both species are available in the culture jars.

2. *Crepidula arenata and C. adunca*

Sometimes in the same tidepools with the two preceding species, but more often offshore, are two other species of *Crepidula* which have a superficial resemblance to each other, particularly when young. These likewise differ in size of eggs and method of development. One of them, *C. adunca* Sowerby (fig. 5) produces a relatively small number of large ova provided with so much yolk that the entire development to the adult form takes place within the egg capsules. The other, *C. arenata* Broderip, deposits at each ovulation a larger number of small ova, about two-fifths the diameter, or one-sixteenth the volume, of those of the companion species, and these develop into pelagic veliger larvae.

Both species are found attached to the outer surfaces of the shells of various gastropods, as well as to rocks and other solid objects. As in the other species mentioned, the size and shape of each individual is influenced by the surface to which it is attached. In some locations *C. arenata* seems to have a preference for the slender, cylindrical shells of *Olivella,* to which the *Crepidula* may conform both in shape and color. When young individuals of that species are cultured in large jars immersed in the ocean for a few months the broadly oval shape of the young shell is retained in the adult.

Young individuals of *C. arenata* are morphologically similar to those of *C. adunca* and have a hooked excavated apex widely separated from the margin at the posterior end of the shell. As growth proceeds the margin approaches the apex more closely. Shells of *C. adunca* are generally brown in color, occasionally with indications of radial stripes, both internally and externally. Those of *C. arenata* are highly variable in color; when young, the shells are commonly light brown or gray with narrow radiating lines of darker, reddish brown. In some, the posterior portion of the shell and the apex are white, with a pair of white lateral bands and a white median band extending toward the anterior margin. Older shells are frequently mottled with reddish brown and white, with a broad white median band from apex to anterior margin. All retain traces of the original radiating stripes. When a hermit crab occupies the shell to which the *Crepidula* is attached, a white median band results from erosion as the shell is dragged about by the crab. When cultured on the inside of glass jars, the median white band is often absent, although it is some-

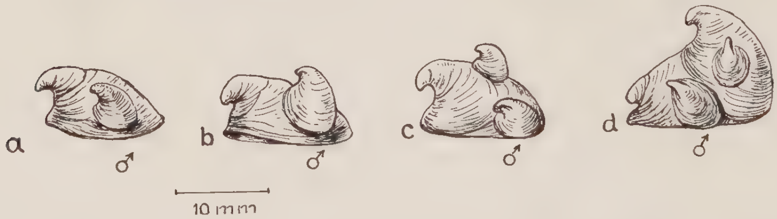

Fig. 5 *Crepidula adunca.* a, b, mated pairs; c, female phase, with mated male and supplementary male; d, two superimposed female-phase individuals each with mated male.

times conspicuous even on the newly deposited portion of the shell.

3. Crepidula norrisiarum and C. onyx

In addition to the two pairs of species mentioned, there may occur in the same tidepools a third pair, the members of which differ in the same respects as the preceding. These species however, have different morphological characteristics and are easily distinguishable when adult. One of them, *Crepidula norrisiarum* Williamson, commonly produces at each ovulation several hundred large ova which complete their development to the adult form within the egg capsules. The other, *C. onyx* Sowerby (fig. 6), usually deposits 5000 to 20,000 small ova at each ovulation and these develop into pelagic veligers which experience a free-swimming life of several weeks before transforming to the adult condition.

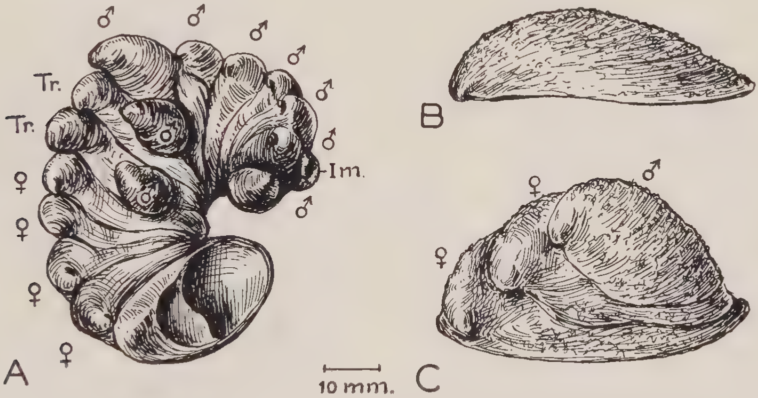

Fig. 6 *Crepidula onyx.* A, typical form from muddy bottom; large group consisting of 17 individuals, 5 in female phase, two in transition stage, 9 in male phase and one sexually immature young. B, C, flat, roughened form *(rugosa)* from hard substrate with unlimited space for growth.

OVULATION AND LARVAL DEVELOPMENT OF SOME AMERICAN CALYPTRAEIDAE

In regard to their mode of development all the species of this family may be divided into two groups, as has been mentioned for the three pairs of California species: *A*, those which produce very numerous small eggs which develop into pelagic larvae, and *B*, those producing a relatively small number of eggs of much larger size which complete development to the adult form while within the egg capsules. Both types have holoblastic cleavage, as described a half century ago by Conklin (1897). The characteristics of the egg clusters and the type of development of the American species insofar as at present known are described below.

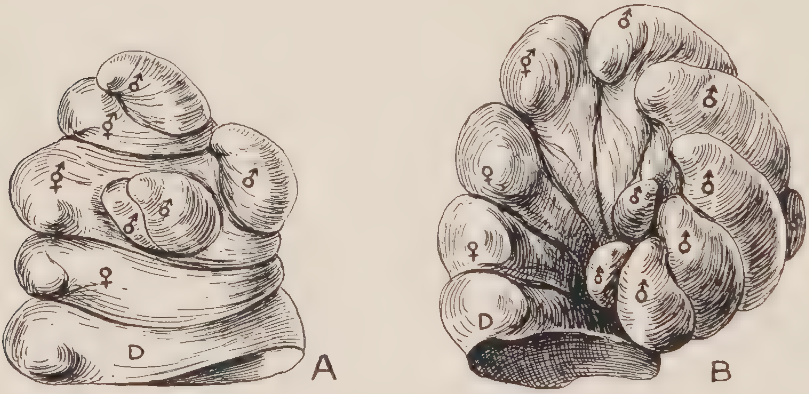

Fig. 7 *Crepidula fornicata.* A, small group consisting of one dead shell *(D)*, one female-phase individual, two individuals in process of sexual transformation and 4 males. B, larger group with two female-phase individuals, one transition individual and 7 males.

Group A. Species with small eggs and pelagic veliger larvae

The species of this group on the Atlantic coast are:

1. *Crepidula fornicata* Lamarck (fig. 7). Large individuals may produce as many as 10,000 to 13,000 ova at each ovulation. These are deposited in 40 to 70 capsules, each containing 120 to 250 ova about 0.165 to 0.18 mm in diameter. The developmental history is similar to that in *C. plana.*

2. *Crepidula plana* Say (fig. 8, B). Large individuals commonly deposit at each ovulation 40 to 50 capsules, each containing 80 to 180 ova, or a total of 5000 to 9000 or more.

Dwarfs produce only 2000 to 3000. Each ovum is 0.13 to 0.14 mm in diameter. After an incubation period of about 4 weeks beneath the parent's foot, the veliger larvae escape into the water and undergo a pelagic life for presumably two to three weeks before transforming to the adult condition (Conklin, 1897). This species has become established in Puget Sound on the Pacific coast where it was introduced with oysters. It is closely similar to, if not specifically identical with, *C. nivea* Adams which is endemic on the Pacific coast. The eggs and the larval development are similar in both.

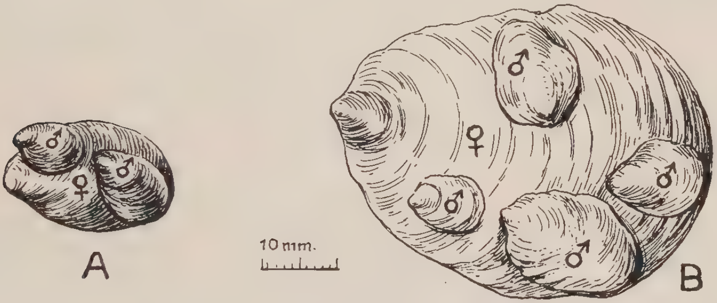

Fig. 8 A, *Crepidula glauca,* female phase with mated males. B, *Crepidula plana,* broad growth form; female phase with mated and supplementary male-phase individuals.

On the Pacific coast the following species have small ova which develop into pelagic veligers:

1. *Crepidula arenata* Broderip. Individuals 13 to 16 mm in length produce 20 to 80 capsules, each with an average of about 25 ova approximately 0.16 mm in diameter, or a total of 500 to 2000 at each ovulation. Some conchologists have considered this species to be conspecific with *C. excavata* Broderip in spite of the much larger size attained by typical examples of the latter, as well as difference in general appearance.

2. *Crepidula fornicata* Lamarck, as mentioned for the Atlantic coast. Introduced with oysters but survival at present is doubtful.

3. *Crepidula (Crepipatella) lingulata* Gould (fig. 9). The number of capsules is usually 7 to 20, each with 100 to 400 small ova, or a total of 2000 to 6000 at each ovulation. The ova are about 0.15 mm in diameter and produce pelagic veligers.

4. *Crepidula nivea* Adams (fig. 2). Dwarf individuals inhabiting the shells of *Tegula* commonly deposit at each ovulation 20 to 30 capsules each with 50 to 80 ova, or a total of 1500 to 2000. Large individuals which have had space for continued growth may produce more than 8000. Each of these is about 0.13 to 0.14 mm in diameter. The egg clusters are deposited at intervals of about two months.

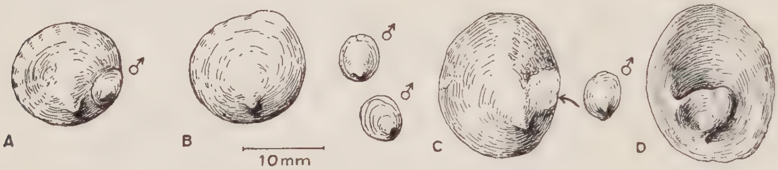

Fig. 9 **Crepidula lingulata.** A, mated pair; B, female phase with two not closely associated males; C, female and male phases; D, shell from ventral side to show character of internal septum.

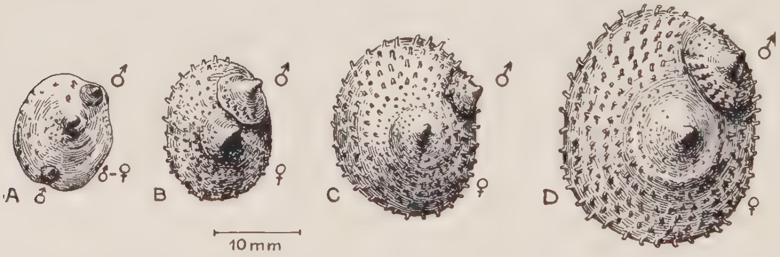

Fig. 10 **Crucibulum spinosum.** A, transition phase with two small, male-phase individuals attached; B, C, D, mated pairs of increasing size.

5. *Crepidula onyx* Sowerby *(C. rugosa* Nuttall) (fig. 6). The number of capsules is commonly 50 to 100, each containing 100 to 200 ova, or a total of 5000 to 20,000 at each ovulation. On the coast of southern California there may be 6 to 8 ovulations in a year. After an incubation period of about three weeks in summer and 4 weeks in winter, the eggs, which average 0.172 mm in diameter, produce typical pelagic larvae.

6. *Crepidula plana* Say, as mentioned for the Atlantic coast.

7. *Crucibulum spinosum* Sowerby (fig. 10). The ova are deposited in 6 to 30 or more capsules at each ovulation. There are usually 60 to 150 yellowish ova, 0.17 to 0.19 mm in diameter, in each capsule, or a total of 500 to 4000 or more. The pelagic veligers leave the capsules after an incubation period of three to 4 weeks, depending on the temperature. Successive ovulations may occur at intervals of 6 to 8 weeks (Coe, '38b).

Group B. Species with large eggs and non-pelagic larvae

The representatives of this group on the Atlantic coast are:

1. *Crepidula aculeata* Gmelin. This species is found in low latitudes over the entire circumference of the earth. The egg clusters usually consist of 8 to 12 capsules, each with 8 to 12 large ova, or a total of 80 to 130 or more.

2. *Crepidula glauca* Say (fig. 8, A). This name has page priority over the more commonly used *C. convexa* Say. Instead of the thousands of small eggs produced by large individuals of *C. plana* and *C. fornicata* at each ovulation, the egg clusters of *C. glauca* seldom contain as many as 250. These are commonly deposited in 15 to 25 capsules, each containing 8 to 20 ova about 0.28 mm in diameter. The large amount of yolk enables the larvae to complete their development to the adult form while in the capsules. There is some cannibalism, however, for the number of young at the time of leaving the capsule is smaller than the number in the earlier stages of development. This species has been introduced and has become established in San Francisco Bay.

Representatives of this group on the Pacific coast include:

1. *Crepidula aculeata*, as mentioned for the Atlantic coast.

2. *Crepidula adunca* Sowerby (fig. 8). The egg-masses of this species seldom contain more than 8 to 12 capsules, each with 15 to 25 ova, or a total of 150 to 250. The ova are about 0.4 to 0.42 mm in diameter.

3. *Crepidula glauca*, as mentioned for the Atlantic coast.

4. *Crepidula norrisiarum* Williamson. The egg clusters of individuals more than 25 mm in length usually consist of 16 to 25 capsules, each with 15 to 30 yellow ova or a total of 200 to 500 or more. The eggs average about 0.5 mm in diameter.

5. *Crepidula williamsi* Coe (figs. 3, 4). Dwarf individuals, 14 to 17 mm in length, commonly produce at each ovulation 7 to 12 capsules, each with 8 to 20 ova or a total of 50 to 200, while a single egg cluster of a large individual 20 to 30 mm in length may contain as many as 30 to 40 capsules with an average of 21 ova or a total of 600 to 700 or more. The eggs are about 0.45 mm in diameter.

6. *Crepidula perforans* Valenciennes (*C. exuviata* Nuttall). Individuals of this species, with thick, narrow, frilled shells, occupy holes bored by pholads in hardened clay and rocks. The eggs before cleavage are about 0.5 mm in diameter but the larvae before hatching reach a length of 0.8 mm or more.

Information relative to ovulation and larval development of other American Calyptraeidae must await further investigation. Some of the species from other parts of the world likewise have pelagic and others non-pelagic larvae. Those of *Crepidula walshi* on the coast of Japan are pelagic, while those of *C. aculeata* in the same locality are non-pelagic. Similar differences are found in *Capulus ungaricus* and *Calyptraea sinensis* of European shores and have been reported for the snails *Polinices heros* and *P. triseriata* of the North American Atlantic coast.

Thorson ('46) shows that in some other Prosobranchs, species with small eggs and pelagic larvae occur in the same genus with other species that have much larger eggs and a non-pelagic type of development. Several species produce larvae which are pelagic for only a few hours or a few days but in the majority of species the larvae experience a pelagic life of several weeks. Both pelagic and non-pelagic larvae may occur in the same species in those cases where the eggs are provided with a varying number of nurse cells. And finally there may be local races which differ somewhat in size of egg and mode of development.

The species which produce large numbers of small, free-swimming veligers would seem to have some advantage over those with fewer, but larger, young which are incubated within the egg capsules beneath the parent's foot. This is indicated by the fact that in most geographical areas the individuals of the species with pelagic larvae are of larger size and the populations are generally much more numerous and more widely dispersed than in the species with the non-pelagic larvae. Thorson ('46) states that among the 61 species of Prosobranchs, of which the larval life is known, found on the coast of Denmark, two species are viviparous, 19 have non-pelagic larvae, 5 have larvae with a short pelagic life and 35 have a long larval life in the plankton.

Thorson ('40) has also presented evidence that pelagic larvae are more characteristic of warm, rather than of colder regions. About 75% of the Prosobranchs examined in the Iranian Gulf have pelagic larvae, although no example of that type of development has been found among the Prosobranchs in the cold waters of the Arctic, Antarctic or the deep oceans.

COMPARISON WITH OTHER GROUPS OF MOLLUSKS

Although the foregoing examples of morphologically similar species producing different types of eggs with divergent methods of development are unusual, they are by no means unique. Similar conditions are found in other groups of mollusks, as well as in many other animals. Among the oysters, for example, are some species that are larviparous and others, formerly considered as belonging to the same genus that are oviparous. The former are characterized by the production of a comparatively small number of relatively large eggs which are retained in the mantle cavity until the larvae have reached the primitive-shelled, or prodissoconch, stage. Each large, female-phase individual of the latter group discharges into the water 1,000,000 to 50,000,000 very small eggs which are fertilized outside the body and develop into typical pelagic veligers. Species of the two groups are now generally assigned to separate genera, *Ostrea* and *Crassostrea,* respectively. Individuals of former genus, like *Crepidula,* are generally, but not invariably, protandric, but unlike *Crepidula* commonly experience alternating phases of male and female sexuality throughout life.

A similar condition may be mentioned for another group of mollusks. On the coast of southern California there are evidently two morphologically similar species of *Octopus.* One of these produces eggs which have about 8 times the volume of those of the other species, although, insofar as the writer knows, no morphological distinctions between them have yet been found, other than in the reproductive system of the female. These two types of eggs have sometimes been thought to indicate separate genera. Even if other morphological differences are not found, it would not be in harmony with the species concept to think that individuals with such diverse methods of reproduction could belong to a single species.

SUMMARY

On the coast of southern California there are 6 species of gastropods belonging to the genus *Crepidula* which may be considered as forming three contrasting pairs. The two members of each pair are closely similar morphologically but differ in size of eggs and mode of development. One species of each pair produces relatively few large eggs that have sufficient yolk to enable them to complete development to the adult form while within the egg capsules beneath the foot of the parent. In the companion species the much more numerous small eggs develop into pelagic veliger larvae which experience a free-swimming life of several weeks before transforming to the adult form. The type of egg and mode of development may be more reliable criteria of the species than the highly variable and often intergrading external morphological features.

The egg clusters of each of the American species are described, insofar as they are at present known, and the type of larval development recorded. As indicated by extent of

geographical distribution and size of individuals and of populations, the species with free-swimming veligers would seem to have some advantages over those with non-pelagic larvae in regions of warm or moderate temperatures. Of the 13 American species mentioned, 7 have pelagic and 6 non-pelagic larvae.

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Contribution No. 418

THE CONCEPTION OF ALKALINITY OR EXCESS BASE OF SEA WATER[1]

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There is full agreement on these facts: Sea water is slightly alkaline in its reaction towards suitable indicators, and the quantitative measure of this alkalinity may be expressed in terms of the amount of strong acid necessary to bring its reaction to some standard specified "endpoint." We call this property "alkalinity" if we describe the experimental phenomenon, or call it "excess base" if we try to interpret the observed facts and ascribe a cause. The term "buffer capacity" is unfortunate and should be dropped entirely.

It is proper to seek the cause of this property in what may be called the acid-base balance of the water, but there is a common misapprehension as to what we are talking about, because in chemical oceanography we are still clinging to conceptions which have been abandoned and replaced in the field of general chemistry. To be sure, the same misapprehension persists elsewhere, in some of the other applied fields of chemistry.

To illustrate the nature of the difficulty, let us examine some of the statements which appear in the literature.

Harvey, in his *Biological Chemistry and Physics of Sea Water*, says:

> The bases in sea water are slightly greater than the equivalent of stable acid radicals; there is a portion of *excess base or "alkali reserve"* which is in combination with carbonic acid. (Harvey, 1928: 64).

Later, in his *Recent Advances in the Chemistry & Biology of Sea Water* the same author states:

> The water contains basic radicles in excess of the equivalent of strong acid radicles. This excess base is itself equivalent to the bicarbonate, carbonate and borate ions in the water (Harvey, 1945: 52).
>
> Furthermore, some of the excess base becomes "bound" to borate ions which are set free from undissociated boric acid (Harvey, 1945: 54).
>
> The term 'Carbonate alkalinity' is used for that part of the excess base which is equivalent to the bicarbonate and carbonate ions (Harvey, 1945: 61).

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[1] Contributions from the Scripps Institution of Oceanography, New Series, No. 418.

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In the recent comprehensive textbook, *The Oceans*, we find:

> For a given sample of sea water the amount of a strong acid (usually HCl about 0.01 normal) necessary to reduce the pH to about 4.5 is independent of the total CO_2. This amount of acid is required to set free the weak acids whose anions have been bound against basic cations. It is therefore not only a measure of the quantity of anions of weak acids in the sample, but also of the cations balanced against them (Sverdrup, Johnson and Fleming, 1942: 195).

From Kalle's *Der Stoffhaushalt des Meeres:*

> Von einer gewöhnlichen Salzlösung, beispielsweise einer Kochsalzlösung, unterscheidet sich das Meerwasser in einem wesentlichen Punkt. Während in einer gewöhnlichen Salzlösung im allgemeinen die Menge der Kationen derjenigen der Anionen äquivalent ist, ist im Meerwasser diese Beziehung, soweit wir uns auf die Betrachtung der Ionen starker Basen und Säuren beschränken, nicht erfüllt. Wie Tabelle 7 (S. 38) zeigt, haben wir einen Überschuss von 2.38 Milliäquivalenten an Kationen pro kg Meerwasser (Kalle, 1945: 158–159).

Wattenberg not only defines excess base but relates the calcium ion concentration ion closely to it:

> Die Summe der im Meerwasser vorhandenen Kationen übertrifft nämlich die Summe der Anionen starker Säuren—beide ausgedrückt in Äquivalenten—um einen gewissen Betrag. Dieser "Basenüberschuss" ist die an Kohlensäure (als Karbonat und Bikarbonat) gebundene Basenmenge. Wird nun dem Wasser $CaCO_3$ entzogen oder zugeführt, so wird dadurch eine äquivalente Verminderung bzw. Vermehrung des Basenüberschusses, der sog. Alkalinität verursacht. Dieser Kalkstoffwechsel ist nun praktisch die einzige Ursache für die Veränderungen in der Alkalinität des Meerwassers, und es ist daher umgekehrt möglich, aus der Alkalinität den zugehörigen $CaCO_3$-Gehalt des Wassers zu berechnen (Wattenberg, 1930: 278).

In their paper *The Buffer Mechanism of Sea Water*, Moberg, Greenberg, Revelle and Allen say:

> By titratable base we mean the base balanced against weak acid radicals in sea water, or, stated in another way, the quantity of base which can be titrated with a strong acid when the titration is carried to a pH value at which all the weak acid radicals have been replaced by the acid added (Moberg, et al., 1934: 231).

Elsewhere, they refer to

> . . . the portion of the titratable base balanced by carbonic acid . . (Moberg, et al., 1934: 261).

Greenberg, Moberg and Allen express themselves similarly:

> . . . we are using the expression "titratable base" to designate the base combined with weak acid radicals . . . (Greenberg, et al., 1932: 311).

Although West and Robinson (1941) make use of conceptions substantially the same as those which will be explained presently, they do not point out the general implications of them.

The above statements seem to agree on the following points:

1. The cations are bases. [Wattenberg (1930) followed this to a conclusion.]

2. The anions are at least "acid ions," if not actually acids.

3. The anions of weak acids are in some way inactivated by being "bound against" cations. Strong acid "replaces" these ions during the titration.

The tables referred to by Kalle (1945) list the principal cations, Na^+, Mg^{++}, Ca^{++}, K^+, Sr^{++}, in terms of equivalents and compare them with the anions, similarly expressed. The total equivalents of cations exceed the equivalents of anions, *but only if certain anions* (HCO_3^-, $H_2BO_3^-$, $CO_3^=$) *are left out of the list.*

In any electrolyte solution, of course, total anions equal total cations. What justification is there for neglecting the anions of weak acids? Just what is meant by "balancing" or "binding against"? How is this different from "binding with"? In at least three of the sources quoted above it is explicitly stated that some of the cations are *combined with* anions. If this were the case, the inactivation of the weak acid ions should also inactivate an equivalent of cations, and there would be no excess of base. But the idea of undissociated salt molecules (such as $NaHCO_3$ or KH_2BO_3) went out of style in physical chemistry some years ago. The current picture of an electrolyte solution, such as sea water, is one in which ions retain their independence rather than pair off with each other, although there is a diffuse interionic attraction of all the positive ions for all the negative. And there is no reason why a cation should be bound "against," or "by," or "with," an anion like bicarbonate any more than one like chloride.

The difficulty arises from the inconvenience, or utter failure, of our old ideas about the relation of acid to base. The same difficulty led to confusion in a totally different field, that of the so-called "ion-exchange" substances.

Certain natural and synthetic substances—first zeolites, and more recently certain resins—when immersed in solutions have the property of yielding up certain ions which they contain in exchange for other ions in the solution. The first of these substances were originally known as "base exchangers," since they exchanged sodium or potassium ions for calcium or magnesium. Others, later discovered, were called "acid exchangers" since they could exchange anions (then called "acid ions").

But presently it developed that the "base exchangers" could exchange calcium ions not only for sodium *but even for hydrogen ions*, which, according to the classical definition, is the one and only *acid.* Further, the "acid exchangers" were found to exchange sulfate ions not only for chloride *but even for hydroxyl*, which has classicially been thought the one and only *base.* Surely, acid cannot be exchanged for base!

All this confusion can readily be cleared up by turning to a revision which has taken place in recent years in our fundamental conceptions of acids and bases. The modern definitions or theory of acid and bases, although more general than the classical, afford much simpler explanations. We shall use such portions of the modern theory as are useful for our present purpose.

The properties of acids are ascribed to the unique character of the proton, or simple hydrogen ion (H^+), which, because of its small size, differs from other cations, the metals in general. The proton forms stable, individual unions with cations; with chloride, for example, the product HCl is a gas with a real molecular weight. (Contrast this with solid sodium chloride, in which no sodium ion is united with any particular chloride ion.) The proton is not irrevocably bound in such unions, however, but can separate to attach itself to any other entity (ion or neutral molecule) with which it forms a firmer union. Acids are defined as "proton donors" from which protons (H^+) can separate in this way. Protons separate *easily* from strong acids (HCl), with difficulty from weak ones (H_2CO_3).

Bases, on the other hand, are defined as "proton acceptors," substances (ions or neutral molecules) which can combine with protons. Protons form strong unions with strong bases, weak ones with weak bases.

It is evident from this that all anions are bases and that an acid *consists of a proton united with a base.* In a strong acid, like HCl, the proton is united with a weak base (Cl^-); in a weak acid, like H_2CO_3, the proton is united with a strong base (HCO_3^-, or $CO_3^=$, since two protons are involved).

Water itself is a weak base, combining with the proton of a strong acid, like HCl, to form Cl^- and H_3O^+, the hydronium ion or the hydrated proton. Water is also a weak acid, able to yield protons to strong bases, like $S^=$, or $CO_3^=$, or NH_2^- (to form HS^-, HCO_3^-, NH_3). All these exchanges are reversible, of course, and protons will distribute themselves between any bases that are present, in proportion to their strengths. It will be useless to go further into the details of these conceptions, which can be found in many modern textbooks of chemistry.

It should be noted that metal ions in solution (and doubtless all ions) are hydrated. For example, the cupric ion has the composition $Cu(H_2O)_4^{++}$, and the ferric $Fe(H_2O)_6^{+++}$, although there is some uncertainty about the number of water molecules coordinated in some cases. In a real sense, $Cu(H_2O)_4^{++}$ is a hydrogen compound containing protons, and elementary considerations of atomic structure would indicate that protons should be more easily separated from it than from the H_2O molecule. One must think of the water molecule as two protons, each of which is attached to an oxygen atom by sharing a pair of electrons. The oxygen atom has two more pairs of electrons, by which it can be "coordinated" to other atoms, molecules, or ions. When metal ions coordinate with water molecules in this way, the sharing of these electrons with the oxygen atom tends to draw in slightly the electrons which hold the protons to the oxygen. This loosens the H : O bond slightly and enables a proton to separate from the oxygen more easily than it will from an oxygen atom in an independent water molecule. Consequently, the "hydrated" metal ions have the properties of acids. Small ions, like iron and copper, coordinate the water molecules strongly and are therefore relatively strong acids; sodium or potassium, and other large ions, scarcely "polarize" the water molecules at all and are hardly any more effective as proton donors than water itself.

In place of the old classification, according to which cations and anions are considered "base ions" and "acid ions" respectively, the true situation is actually reversed: cations are in general *acids*, and anions in general *bases*.

Now it can be readily understood that in a water solution containing $Cu(H_2O)_4^{++}$ and Cl^- ions there is a predominance of acid over base. Although their equivalent concentrations will be the same, the copper ion is more effective as an acid than is the chloride as a base. It can yield a proton to an added indicator more readily than the chloride will take one from the indicator, and the well known color change takes place. The solution contains "excess acid."

In a solution containing $Na(H_2O)_x^+$ and HCO_3^- ions, the bicarbonate is more effective as a base than the sodium (in equivalent concentration) as an acid, the solution has an alkaline reaction, and we have all the evidences of *excess base.*

In a neutral solution of sodium chloride we have not only equivalent concentrations of anion and cation but also equal acid and base effectiveness. (The term "activity" must be avoided, since it has another technical significance.)

"Excess base," therefore, refers more particularly to relative acid and base strength than to relative concentration. We can now deal with the actual situation in sea water.

The cations (acids) present are: $Na(H_2O)_x^+$, $Mg(H_2O)_x^{++}$, $Ca(H_2O)_x^{++}$, $K(H_2O)_x^+$, $Sr(H_2O)_x^{++}$. (The water of hydration is usually omitted when writing the formulas.) Of these only the magnesium ion has any appreciable power as an acid, and even this is too small to be significant. Cations which might be effective acids, $Fe(H_2O)_6^{+++}$ or $Cu(H_2O)_4^{++}$, and of course H^+ (or H_3O^+), are in too low concentration to be important. The anions (bases) present are: Cl^-, $SO_4^=$, Br^-, HCO_3^-, $H_2BO_3^-$, $CO_3^=$. The first three are too weak as bases to be significant; it is to the last three that the alkalinity of the water is due. Phosphate and silicate ions, moderately strong bases, are in insignificant concentration.

The "alkalinity" of the water is the result of the predominance of base effectiveness over acid effectiveness. When we titrate by adding HCl we choose an endpoint at which the HCO_3^-, $H_2BO_3^-$ and $CO_3^=$ are completely combined with protons to form H_2CO_3 and H_3BO_3. Only the relatively strong acids and bases are involved, so that chloride, bromide, sulfate, and the principal metal cations are unimportant. Hydrogen and hydroxyl ions, although respectively strong acid and base, are too dilute. So that, finally, our definition of excess base, in terms of equivalents of acid added,

$$A = [HCO_3^-] + 2\,[CO_3^=] + [H_2BO_3^-]\,,$$

is an exact definition of what we *mean* by excess base, not something which is merely *equivalent* to it.

This is entirely incompatible with Gripenberg's (1936) statement that while the quantities on the right of the above equation vary with the hydrogen ion concentration the excess base is independent of it. Her statement is the result of assuming that excess base is a *cation concentration* and it is hard to see how it can be true even according to the older view. Our criterion of the presence of excess base is the fact that acid must be added to the water to bring the pH to an endpoint of, say, 5. Obviously, if the original pH of the water were 5, by definition there would be no excess base in it.

Finally, the effect of calcium carbonate precipitation upon the alkalinity is the result of the removal not of calcium ions but of carbonate, which of course is chemically equivalent.

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Contribution No. 419

Possible Part Played by Bacteria in Petroleum Formation

Abstract of talk given by Dr. Claude E. ZoBell, Scripps Institution of Oceanography, University of California, La Jolla, before the Southern California Section of the American Chemical Society May 6, 1949

Petroleum is a complex mixture of gaseous, liquid and solid hydrocarbons of the paraffinic, aromatic or naphthenic series. Small amounts of high molecular weight compounds of nitrogen, oxygen, sulfur and phosphorus are also usually present. Petroleums from different fields differ greatly in chemical composition, density, viscosity, color and other properties.

In view of the strategic and ever-increasing importance of oil to our modern mechanized and martialized civilization, it is an anomalous situation that so little is known regarding what petroleum is and how it was formed. There are almost as many theories to account for the origin of oil as there are students of the subject. Most authorities, however, agree that petroleum probably was formed from the organic remains of plants and/or animals. Assuming that petroleum has had an organic origin, it is axiomatic that bacteria have contributed to the process because following death the bodies of all kinds of plants and animals are susceptible to bacterial attack.

Living bacteria have been shown to be widely and abundantly distributed in marine sediments where oil is found and where it is believed to have been formed. These bacteria will tolerate temperatures, salinities, hydrostatic pressures and other environmental conditions characteristic of petroliferous sediments.

Bacteria produce a formidable array of enzymes or biocatalysts which catalyze a great many chemical reactions involving both organic and inorganic materials. Virtually all types of organic compounds are attacked by bacterial enzymes.

In nature bacteria may modify organic matter in four general ways, depending primarily upon the environmental conditions: oxidation, humification, carbonization and hydrogenation. Oxidation, which may take place under either aerobic or anerobic conditions, tends to convert organic compounds into carbon dioxide, water and other simple substances. Humification commonly occurs in soil and submerged sediments. Bacteria and allied microorganisms contribute to the carbonization of organic matter in peat deposits by processes which decrease the H:C ratio. In the conversion of organic compounds into petroleum hydrocarbons there is an increase in the H:C ratio of the reduced residuum.

In certain marine sediments where conditions are highly reducing (low redox potential), bacteria tend to eliminate nitrogen, oxygen, sulfur and phosphorus from organic matter, leaving a residuum that is relatively richer in hydrogen and carbon. Although the total quantity of organic matter in sedimentary materials may decrease as a result of the activities of anaerobic bacteria, the percentage of hydrogen and carbon in the residuum increases until it approaches the proximate chemical composition of petroleum. This has been demonstrated by laboratory experiments and also found in profile series of marine sediments from increasing core depths.

Hydrocarbons are produced by certain bacteria. Methane, a common constituent of natural gas and crude oil, is produced during the anaerobic fermentation of many different organic compounds. Traces of ethane and propane are also produced. Liquid and solid paraffinic hydrocarbons ranging from $C_{16}H_{34}$ to $C_{31}H_{64}$ as well as small amounts of naphthenic hydrocarbons have been detected in the cell substance of anaerobic bacteria. From tyrosine and phenylalanine bacteria produce phenol and cresol, hydrocarbon-like substances commonly occuring in crude oil. Although not found in crude oil, it is significant that carotene, leprotene, flavorhodin and other pigmented unsaturated hydrocarbons are produced by bacteria.

Bacteria may contribute to petroleum formation either by the production or by the utilization of molecular hydrogen. Certain anaerobes which produce an enzyme called hydrogenase are able to catalyze the reaction of molecular hydrogen with various unsaturated organic compounds. Hydrogenase may also catalyze the reduction of sulfate or carbon dioxide in the presence of molecular hydrogen, e.g.:

$$CO_2 + 4\ H_2 \rightarrow CH_4 + 2\ H_2O$$

Under the influence of alpha particles from radioactive constituents found in marine sediments, methane may be converted partly into ethane, propane, butane and higher hydrocarbons. Hydrogen liberated during the reaction may help to account for the hydrogen required for the reduction of organic compounds to hydrocarbons, although molecular hydrogen is also produced by certain chemical reactions in the earth's crust as well as by bacteria which ferments organic compounds. The tendency of hydrogenase-producing bacteria to catalyze the reaction of molecular hydrogen with other substances may explain the low content of free hydrogen in natural gas.

Another function of bacteria is to lower the redox potential of sedimentary deposits. Anaerobic bacteria growing in marine sediments tend to create reducing conditions which are favorable for the formation and preservation of hydrocarbons. Source sediments of petroleum have been found to be highly reducing, a characteristic which is attributable to the action of bacteria.

Perhaps one of the most important contributions of bacteria to the origin of oil has been in releasing oil absorbed on sedimentary particles and promoting its flow to structural or strategic traps. Test tube experiments have demonstrated that bacteria may release oil and promote its flow in several ways: (a) By decomposing organic matrix which contains oil, (b) By dissolving sulfate rocks such as gypsum or anhydrite holding adsorbed or interstitial oil, (c) By dissolving oil-bearing carbonate rocks such as limestone or anhydrite, (d) By producing carbon dioxide which tends to decrease the viscosity of oil, (e) By producing hydrogen, methane or other gases which force oil out of micro-traps or through capillary spaces, (f) By producing surface-active substances or detergents which lower the surface tension of water, and (g) By crowding oil off surfaces owing to the tendency of thigmatactic bacteria to grow on solid surfaces.

Since virtually all types of hydrocarbons are susceptible to bacterial attack, bacteria may modify petroleum in various ways. They may alter the properties of the oil or they may destroy petroleum hydrocarbons in certain environments. More information on the environmental and geochemical factors which influence the bacterial oxidation of oil may provide important clues to what constitutes a source bed of petroleum.

Many commercial petroleum products stored in contact with water may be discolored or otherwise modified by bacteria which attack hydrocarbons. The production of fatty acids, alcohols, ketones, vitamins, antibiotics, etc., by bacteria from petroleum hydrocarbons is an important field for exploitation. The activity, presence and products of bacteria which oxidize volatile hydrocarbons in soil overlayering subterranean deposits of petroleum may serve as indicators in geomicrobiological prospecting methods.

Besides finding applications in the fields of petroleum and chemical technology, the results of research on bacteria as biochemical and geochemical agents are yielding fundamental information on bacterial physiology. The investigations have been sponsored by the American Petroleum Institute as a part of Research Project 43.

Contribution No. 420

FISHES OF ISLE ROYALE, LAKE SUPERIOR, MICHIGAN *

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INTRODUCTION

THIS paper on the fish fauna of Isle Royale (Fig. 1) is meant to serve several purposes. In the first place it is a contribution to the long-continued ichthyological survey of the State of Michigan. Toward this end the record stations for each species have been added currently to our distributional spot maps of the state. It is likewise a contribution to the analysis of the fish fauna of the Great Lakes. Some of the data have been utilized in our preliminary general treatises on that fauna (Hubbs and Lagler, 1939, 1941, 1947). This study also bears on problems of postglacial reinvasion, dispersal, faunal origin, isolation, and speciation, and in this way transcends the restricted limits of systematic ichthyology. Finally, this publication makes known a major segment in the fauna of one of our national parks. As such we hope it may con-

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* Contribution from the Museum of Zoology and the Department of Zoology of the University of Michigan and from the Institute for Fisheries Research of the Michigan Department of Conservation. Contributions from the Scripps Institution of Oceanography, New Series, No. 420.

tribute to the wise management, preservation, general appreciation, and further study of an important recreational and cultural resource.

Field Work, Collections, and Hydrographic Observations

Knowledge of the fish fauna of Isle Royale stems from several field studies. Some fish collections were made on the state geological and natural history survey expeditions of 1904 and 1905, which were reported upon by Ruthven (1906, 1909). The field work of these early parties was limited to some bays and coves and to a few inland lakes and streams. Several additional specimens were collected by Captain R. E. Ellsworth while on a fish patrol in 1920—in McCargoe Cove on August 12 and at the mouth of Washington River (at the Washington Club) on September 14.

An intensive study was made of the inland lakes and their fish faunas by Walter Koelz in 1929, as part of the scientific survey of Isle Royale that was conducted by the University of Michigan under a grant from the Fifty-fifth Legislature of the State of Michigan. Koelz's detailed report remains unpublished but has been extensively utilized in the preparation of this paper. A summary of the characteristics of each lake (Table I) and the list of the fishes present in each (Table IV) are drawn largely from Koelz's work. Hubbs collaborated with Koelz in the identification of the fishes that he collected, other than Coregonidae. An account of the coregonids, together with a brief description of the lakes that harbor them, was published by Koelz in 1931. In the field work he was assisted by George Stanley and John Brumm. In 1930 Stanley investigated the late geological history of the island, with particular reference to sequence of stages of the glacial Great Lakes. He collected a total of nine species at seven localities. Supplementary data were obtained from the commercial fishery reports to the Michigan Department of Conservation and, by verbal communication, from John Van Oosten, who in 1927 conducted a brief reconnaissance of the fisheries of the island and has kindly made his information available to us. H. F. Johnson furnished Van Oosten with a number of records and with data on the past abundance of commercial species. The commercial fishery reports of the U. S. Fish and Wildlife Service were also used, with the coöperation of Ralph Hile.

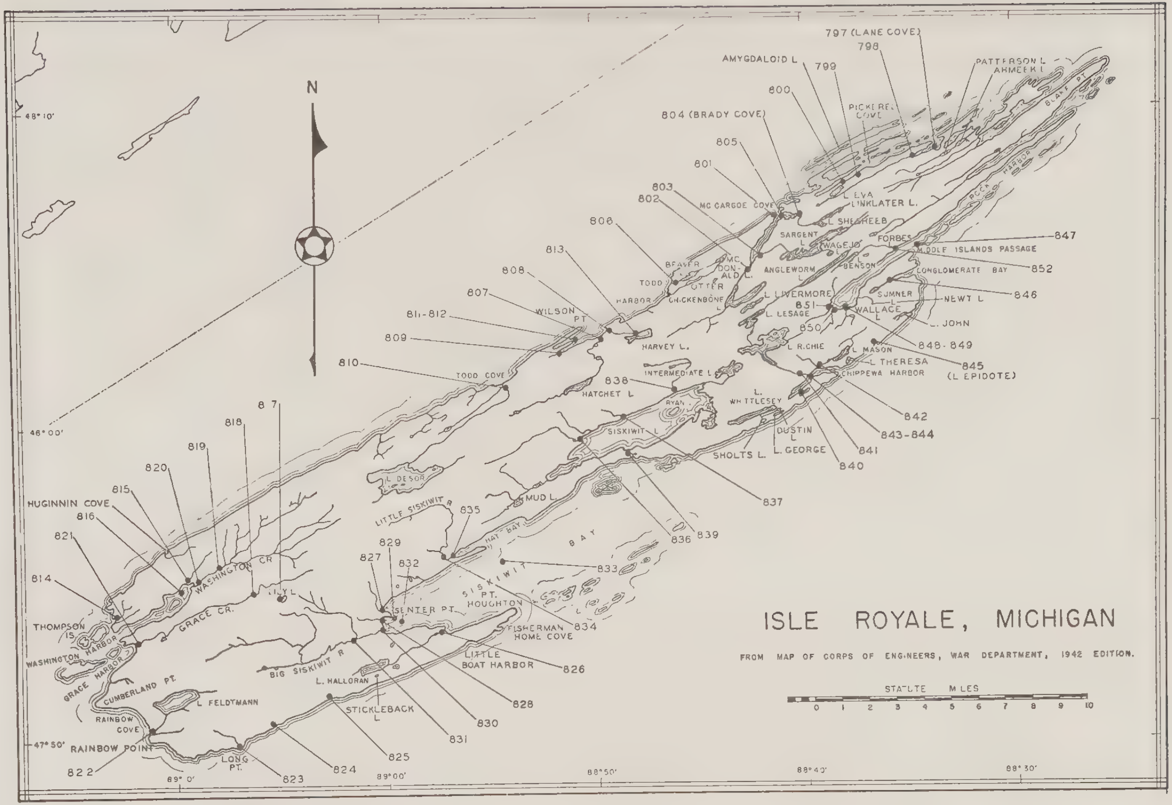
ISLE ROYALE, MICHIGAN
FROM MAP OF CORPS OF ENGINEERS, WAR DEPARTMENT, 1942 EDITION.
STATUTE MILES
0 1 2 3 4 5 6 7 8 9 10
N
48° 10'
48° 00'
47° 50'
89° 0'
89° 00'
88° 50'
88° 40'
88° 30'
797 (LANE COVE)
798
799
800
AMYGDALOID L
PATTERSON L
AHMEEK L
PICKEREL COVE
804 (BRADY COVE)
805
801
803
802
MC CARGOE COVE
L. EVA
LINKLATER L.
L. SHESHEEB
SARGENT L
WAGEJO L
FORBES
847
MIDDLE ISLANDS PASSAGE
852
CONGLOMERATE BAY
846
BENSON
ANGLEWORM L
MC DONALD L.
BEAVER
OTTER
CHICKENBONE L
TODD HARBOR
806
813
808
807
811-812
809
810
WILSON PT
HARVEY L.
L. LIVERMORE
851
L. LESAGE
850
SUMNER L
NEWT L
WALLACE L
L. JOHN
848-849
L. RICHIE
L. MASON
L. THERESA
845 (L EPIDOTE)
CHIPPEWA HARBOR
842
843-844
841
840
INTERMEDIATE L
838
HATCHET L
RYAN L
L. WHITTLESEY
DUSTIN L
SHOLTS L.
L. GEORGE
SISKIWIT L
837
839
836
TODD COVE
L. DESOR
MUD L.
LITTLE SISKIWIT R
835
HAY BAY
SISKIWIT BAY
833
834
829
827
832
SENTER PT.
PT. HOUGHTON
FISHERMAN HOME COVE
LITTLE BOAT HARBOR
826
828
830
831
L. HALLORAN
STICKLEBACK L
BIG SISKIWIT R
825
824
823
LONG PT.
L. FELDTMANN
CUMBERLAND PT.
RAINBOW COVE
RAINBOW POINT
822
GRACE HARBOR
WASHINGTON HARBOR
THOMPSON IS.
814
821
816
815
HUGINNIN COVE
820
819
818
817
WASHINGTON CR
GRACE CR.
LILY L
BLAKE PT
ROCK HARBOR

FIG. 1. Isle Royale, Michigan, showing lakes and streams and the stations (L 45:797 to L 45:851) where fishes were collected in 1945

Aided by a grant from the Horace H. Rackham School of Graduate Studies, University of Michigan, Lagler undertook during the summer of 1945 an expedition to supplement the previous fish collecting on Isle Royale. This field work was conducted as a part of the general fish survey of the state and as one element in Lagler's analysis of the fish fauna of the islands in the Great Lakes. M. E. (Fitzgibbon) Dimick and D. L. (Lundstrom) Puranen effectively assisted in the operations. The National Park Service extended collecting privileges, and the work on the island was expedited by Park Superintendent George Baggley and by Ranger Naturalist Karl Gilbert. The 1945 collections are listed below and are spotted on Figure 1. Supplementary records of larger species of fishes were provided by Karl Gilbert and by Fire Guard George Allen.

DATA ON COLLECTIONS MADE IN 1945 [1]

797. West arm of Lane Cove. Gill-net set at depth of 50 feet. July 15–16, overnight.

798. Stream entering west end of Lane Cove and Lane Cove at mouth of stream. Cedar swamp upstream with beaver dams. Seined to depth of 2 feet. July 17.

799. Small cove opening into Pickerel Cove, about 1,500 feet from mouth of Pickerel Cove. Bottom: silt, with aquatic plants. Seined to depth of 2 feet. July 17.

800. Outlet of Lake Eva into Pickerel Cove. Bottom: rock, silt, and detritus, with sparse aquatic plants. Seined to depth of 2.5 feet. July 17.

801. Mouths of McCargoe and Brady coves. Bottom: sand, rubble, and boulders, with algae on rocks. Gill-net set at depths from 6 to 30 feet. July 17–18, overnight.

802. Outlet of Chickenbone Lake, from mouth to one-half mile upstream, including small tributary entering from west in this section. Bottom: gravel, rubble, boulders, bedrock, silt, and peat, with some aquatic vegetation. Shore: marsh meadow near mouth; wooded upstream. Seined to depth of 3 feet. July 18.

803. Outlet of Sargent Lake into McCargoe Cove, from mouth to one-quarter mile upstream. Bottom: silt, detritus, and boulders. Shore: densely wooded. Seined to depth of 1.5 feet. July 18.

804. Stream entering east end of Brady Cove, vicinity of mouth. Bottom: pulpy peat, silt, and detritus, with some sedges. Seined. July 18.

805. Shore of Birch Island in McCargoe Cove. Bottom: sand, gravel, rubble, and boulders. Seined. Night of July 18.

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[1] Place names, distances, and drainage pattern mostly follow the map by Corps of Engineers, War Department, Isle Royale, Michigan (published by U. S. Lake Survey Office, 1940; Cat. No. 981). For locations see Figure 1. Collections were made during daylight except as otherwise stated. The numbers are all preceded by the series symbol, L45.

806. Outlet of Beaver Lake into Todd Harbor, from mouth to one-quarter mile upstream. Stream falls about one foot through rubble at mouth. Bottom: sand, silt, and detritus, with some algae and moss. Seined to depth of 10 inches. July 19.

807. Outlet of Hatchet Lake into Todd Harbor, from mouth to three-eighths mile upstream. Bottom: bedrock, silt, and detritus, with some algae and moss. Stream falls rapidly over bedrock at mouth; about one-quarter mile upstream it is impounded and sluggish. Seined to depth of 3 feet. July 19.

808. Outlet of Harvey Lake into Todd Harbor, from mouth to one-quarter mile upstream. Bottom: sand, gravel, silt, and detritus, with no vegetation. The mouth is partly blocked by a beach bar of gravel and detritus. The lower one-eighth mile of the stream is at Lake Superior level. Upstream, the bottom changes to sand and gravel, and there are riffles and pools. Seined to depth of 3 feet. July 19.

809. Stream entering extreme western end of Pickett Bay of Todd Harbor. Bottom: sand, silt, fibrous peat, and detritus, with some water plants. Shore: cedar and alder thicket and swampy. Temperature, 68° F. Seined to 2.5 feet. July 19.

810. Outlet of Lake Desor into Todd Cove to five-eighths mile upstream and small tributary entering this outlet from west near its mouth. Bottom: silt and fibrous and pulpy peat in lower reaches, with some aquatic plants; sand, gravel, and detritus upstream. Seined to depth of 3 feet. July 20.

811. Shore of Taylor Island in Todd Harbor. Bottom: gravel, rubble, and few boulders, with some algae. Seined to depth of 4 feet. July 20, night.

812. Todd Harbor in channel between Florence Point and Taylor Island. Gill-net set at depths from 8 to 22 feet. July 20–21, overnight.

813. Harvey Lake in vicinity of outlet and in outlet near source (Pl. I, Fig. 3). Bottom: sand, gravel, few boulders, silt, and detritus. Shore: waist-high poplars and abundant burned downed timber. Temperatures: air, 70° F.; water, 77° F. Seined to depth of 3 feet. July 21.

814. Cove at western end of Isle Royale just opposite (northeast of) Thompson Island, and small stream entering cove. Bottom: in cove, sand, silt, and detritus; in stream, bedrock and rubble. Steam flow: 15 gallons per minute. Temperatures: stream, 63° F.; lake, 61.5° F. Seined to depth of 3 feet. July 22.

815. Stream entering Washington Harbor about 1,000 feet west of mouth of Washington Creek, in mouth and upstream one-eighth mile. Bottom: sand, silt, gravel, and detritus (including large quantity of wood chips). Seined to depth of 2.5 feet. July 22.

816. Washington Harbor along edge of shoal area at east end. Aquatic vegetation (*Potamogeton* and *Myriophyllum*) moderately dense. Gill-net set at depth of 6 feet. July 22–23, overnight.

817. Lily Lake, about 3 miles east of the easternmost extremity of Washington Harbor. Water: light brown, slightly turbid. Bottom: fibrous and pulpy peat with white water lilies. Shore: encroaching bog mat, backed with cedar swamp; then rising to wooded ground. Estimated area: 14 acres. Seined to depth of 4 feet. July 23. (See p. 90.)

818. Grace Creek, tributary of Grace Harbor, about 4.7 miles upstream from mouth. Bottom: sand, silt, detritus, little rubble, and few boulders, with no vegetation. Banks: densely wooded. Seined to depth of 10 inches. July 23.

819. Washington Creek about one mile upstream from mouth and also near old Windigo Mine. Bottom: clay, silt, sand, gravel, rubble, and detritus. Seined to depth of 2.5 feet. July 24.

820. Washington Creek, from mouth to one-quarter mile upstream. Stream broad and at base level; rising tide causing current to move upstream. Bottom: sand, silt, clay, and detritus. Seined to depth of 3 feet. July 24.

821. Grace Creek from mouth to first beaver dam upstream (about one-quarter mile). Seined to depth of 2.5 feet. July 25.

822. Outlet of Lake Feldtmann at mouth into Rainbow Cove and for one-quarter mile upstream. Bottom: sand, gravel, rubble, and some silt. Temperature of stream, 73° F.; of Lake Superior off mouth of stream, 51° F. Seined to depth of 2 feet. July 25.

823. Stream entering Lake Superior at Long Point. Bottom: silt and gravel. Temperature in stream where wooded, 65° F.; in beach pool, 80° F.; in Lake Superior off mouth of stream, 45.5° F. Seined to depth of 2.5 feet. July 25.

824. Bog pond 100 feet inshore from Lake Superior, about 1.25 miles east of Long Point. Bottom: pulpy and fibrous peat and detritus over gravel. Seined to depth of 2.5 feet. July 25.

825. McCormick Beach Creek, tributary to Lake Superior about 4 miles east of Long Point. Bottom: bedrock, sandstone, and silt. Seined to depth of 1.5 feet. July 25.

826. Outlet of Lake Halloran into Siskiwit Bay from mouth to one-quarter mile upstream. Within 100 feet of shore the stream is dammed by beaver; upstream it is swampy. Bottom: sand, boulders, silt, and detritus. Seined to depth of 2.5 feet. July 26.

827. Tributary of Siskiwit Bay about one-half mile north of Senter Point. Small stream with beach pool at mouth and beaver ponds upstream. Seined to depth of 2.5 feet. July 26.

828. Tributary of Siskiwit Bay at southwest base of Senter Point. Bottom: sand, silt, and detritus. Banks: alder and cedar thicket. Water: brown and stagnant, in disconnected pools. Seined to depth of one foot. July 26.

829. Siskiwit Bay just off Senter Point. Gill-net set to depth of 20 feet. July 26–27, overnight.

830. Big Siskiwit River in mouth and near by in Siskiwit Bay. Bottom: sand, gravel, and detritus. Seined to depth of 3 feet. July 26, night.

831. Big Siskiwit River about 2 miles upstream from mouth. Bottom: sand, silt, gravel, and detritus. Banks: alder thicket. Seined to depth of 1.5 feet. July 27.

832. Siskiwit Bay about 1,000 feet off mouth of Big Siskiwit River. Trolling with brass spoon. July 27.

833. Siskiwit Bay about one-quarter mile off Point Hay. Commercial gill-net set at depth of about 30 feet. July 28.

834. Little Siskiwit River to about one-half mile upstream from mouth into Hay Bay. Bottom: bedrock, gravel, sand, rubble, and boulders. No fish above barrier falls about one-quarter mile upstream from mouth. Seined to depth of 2.5 feet. July 28.

835. Hay Bay at mouth of Little Siskiwit River. Bottom: sand and gravel. Seined to depth of 3 feet. July 28.

836. Tributary entering Siskiwit Lake about 2 miles northeast of extreme western end of lake. Bottom: sand, gravel, and rubble. Temperature: 57° F. Seined to depth of 1.5 feet. July 29.

837. Siskiwit Lake and mouth of small stream entering from north, opposite lake outlet. Bottom: sand, gravel, and rubble. Seined to depth of 1.5 feet. July 29.

838. Stream entering Siskiwit Lake from north, opposite Ryan Island. Bottom: sand, gravel, boulders, bedrock, and detritus. Estimated flow, 75 gallons per minute. A series of small cascades lead to a few large pools at lake level. Seined to depth of 2.5 feet. July 29.

839. Outlet of Siskiwit Lake just downstream from falls at Siskiwit Lake. Bottom: bedrock and rubble. Width: to 50 feet. Current: rapid. Temperature, 72° F. Seined to depth of 1.5 feet. July 29.

840. Chippewa Harbor at its westernmost tributary and in lower reaches of tributary. Bottom: sand, silt, boulders, bedrock, and detritus. Vegetation moderately dense. Seined to depth of 2.5 feet. July 30.

841. Outlet of Lake Richie into Chippewa Harbor, at mouth and for one-half mile upstream. Bottom: in lower reaches, silt and detritus; upstream about one-half mile, sand, gravel, and rubble. Flow: 20 gallons per minute. Seined to depth of 4.5 feet, and fished with rod and line. July 30.

842. Outlet of Mason Lake from mouth into Chippewa Harbor to one-half mile upstream. Bottom: sand, silt, and detritus. Vegetation moderate in sluggish flow at base level. Flow (upstream about one-fifth mile) less than 15 gallons per minute. Seined to depth of 2 feet and fished with hook and line. July 30.

843. Chippewa Harbor about mouth of Lake Richie outlet. July 30, night.

844. Chippewa Harbor at narrows below Lake Richie outlet. Gill-net set at depth of about 30 feet. July 30–31, overnight.

845. Lake Epidote and its outlet about 1.25 miles east of Chippewa Harbor, near Lake Superior shore. Bottom: bedrock, slab rubble, boulders, silt, and detritus. Seined to depth of 2 feet. July 31.

846. Outlet of Sumner Lake into Conglomerate Bay; in bay about mouth and to about one-eighth mile upstream. Bottom: sand, silt, gravel, and detritus. Flow: about 50 gallons per minute. Seined to depth of 1.5 feet. July 31.

847. Middle Islands Passage from Rock Harbor to Lake Superior. Gill-net set at depth of 20–35 feet. July 31—August 1, overnight.

848. Rock Harbor, southwesternmost extremity. Bottom: sand, silt, and detritus. Seined to depth of 3 feet. August 1.

849. Outlet of Wallace Lake into Rock Harbor, from mouth to one-quarter mile

TABLE I

Some Characteristics of Isle Royale Lakes*

The lakes are listed in the order of their maximum depths.

Lake	Approximate elevation above Lake Superior (feet)	Maximum depth (feet)	Length of longest axis	Bottom
Mud	<100	3	½ mi.	Mire
Stickleback	<100	3	600 ft.	Bog
Epidote	<10	5	350 ft.	Bedrock, boulders, sandy mud
Newt	100–200	4+	...	...
Sholts	<100	5	900 ft.	Mud, rock
Theresa	<100	8	¼ mi.	Mire
Ahmeek	<100	10	...	Mud
Feldtmann	<100	10	1½ mi.	Sand, mud
George	<100	10	...	Stony, mud
Halloran	<100	10	1 mi.	Mud, sand, peat, detritus
Wagejo	200–300	10	...	...
Wallace	<100	10	¼ mi.+	Mire
Sumner	<100	12	½ mi.—	Mire
Patterson	<100	13	½ mi.	Mire
Harvey†	168	13	...	Sand, peat, detritus
Benson†	About 190	14	1 mi.	Sand, mud
John	100–200	14	½ mi.	Soft
McDonald	<100	14	½ mi.	Sand, mud
Otter	<100	14	...	Mud, clay, sand
Beaver	<100	17	¾ mi.	...
Hatchet†	145	18	1¼ mi.	Sand, gravel, boulders, mud, snags
Livermore†	190	19	1 mi.—	Gravel, mud, snags, bedrock
Shesheeb	<100	20	½ mi.	Mud
Chickenbone	<100	21	1¾ mi.	Soft, muddy
Forbes†	About 190	21	¼ mi.	Mire, sand, gravel, stone, silt
Linklater	<100	21	1 mi.	Mud
Dustin	<100	22	...	Mud, stone
Eva	<100	24	⅝ mi.	Mud
Intermediate	<100	24	1⅛ mi.	Mud, sand, rocks
Mason	<100	26	1 mi.—	Mud, sand, gravel
Amygdaloid	<100	29	...	Mud, bedrock, rocky
Angleworm†	About 190	30	2¼ mi.	Mud, sand, boulders
Lesage†	About 190	30	⅞ mi.	Muddy
Whittlesey	<100	30	2 mi.—	Soft mud, sand
Richie	<100	39	2 mi.	Soft mud, sand, clay
Sargent	<100	45	2¾ mi.	Mud, silt, sand, bedrock
Desor†	235	55	3 mi.—	Sand, gravel, boulders, clay
Lily	<400	. .	...	Fibrous and pulpy peat, detritus
Siskiwit†	57	142	7 mi.	Silt, rocks, clay, detritus

* Physical features (except elevations) mostly as determined by Walter Koelz in 1929.

† Elevation from levels run by George M. Stanley. Other elevations are approximated from 100-foot contours on the map referred to in footnote 1, p. 76.

upstream. Bottom: near mouth, sand, silt, clay, detritus, and a few boulders; upstream, bedrock and boulders. Seined to depth of 2.5 feet. August 1.

850. Stream entering southwesternmost extremity of Rock Harbor (first tributary west of Wallace Lake outlet). Bottom: sand, silt, and detritus. Several beaver dams in stream. Seined to depth of 2.5 feet. August 1.

851. Stream entering Rock Harbor near its southwestern end (the first tributary northwest of Park Camp Ground). Bottom: sand, silt, and detritus. Seined to depth of 3 feet. August 1.

SUPPLEMENTARY HYDROGRAPHIC OBSERVATIONS MADE IN 1945

Tributaries entering Stockly, Five Finger, and Duncan bays from west were extensively dammed by beaver. Small impoundments and beaver swamps have resulted. July 15–17.

Tributary entering western extremity of Todd Cove was a mere trickle with no fish. July 20.

Beaver Lake outlet was dry. July 19.

Tributary of Lake Superior at Thompsonite Beach dropped at its mouth about 20 feet in a falls impassable by fish. Only newt larvae (*Triturus viridescens*) were found above falls. July 20.

Stream channel entering Huginnin Cove was dry. July 22.

Small stream channel entering cove just south of station 814 (see Fig. 1) was dry. July 22.

Small stream channel entering Grace Harbor about one and five-eighths miles southwest of station 821 was dry. July 25.

Small stream channel tributary to Rainbow Cove about 400 feet south of mouth of Lake Feldtmann outlet was dry. July 25.

Small tributary channel entering Rock Harbor (Newt Lake outlet) just southwest of Sumner Lake was dry. August 1.

Zoogeographical Analysis of the Fish Fauna

As now known, the fauna of Isle Royale includes 49 kinds of fish, representing 41 species, 31 genera, and 14 families. With three exceptions all the species are regarded as native to the waters on and about the island, and even these three have reached the island by natural dispersal from other parts of the Great Lakes. *Petromyzon marinus* has expanded its range through the Great Lakes after it reached these waters by passing through canals. *Osmerus mordax* has spread from relatively recent local stockings. *Salmo gairdnerii irideus* has long been established through the Great Lakes as the result of early stocking by man. Another exotic species, *Salmo trutta fario,* was once introduced, but, fortunately, it failed to become established. Koelz (1929 manuscript) ob-

TABLE II

Numerical and Proportional Representation of the Great Lakes Fish Fauna in the Waters of Isle Royale

Family	Numbers of genera, species, and forms						Percentage occurring on Isle Royale		
	Entire Great Lakes*			Isle Royale					
	Genera	Species	Forms	Genera	Species	Forms	Genera	Species	Forms
Petromyzonidae	3	5	5	1†	1†	1†	33†	20†	20†
Polyodontidae	1	1	1	0	0	0	0	0	0
Acipenseridae	1	1	1	1	1	1	100	100	100
Lepisosteidae	1	2	2	0	0	0	0	0	0
Amiidae	1	1	1	0	0	0	0	0	0
Hiodontidae	1	1	1	0	0	0	0	0	0
Clupeidae	3	3	3	0	0	0	0	0	0
Salmonidae	4	7	11	3	3	4	75	43	36
Coregonidae	3	13	44	3	5‡	9‡	100	38‡	20‡
Thymallidae	1	1	1	0	0	0	0	0	0
Osmeridae	1	1	1	1	1	1	100	100	100
Catostomidae	11	19	23	1§	2§	2§	9§	11§	9§
Cyprinidae	25	49	65	9	13	16	36	27	25
Ameiuridae	5	12	12	0	0	0	0	0	0
Umbridae	1	1	1	0	0	0	0	0	0
Esocidae	1	4	4	1	2	2	100	50	50
Anguillidae	1	1	1	0	0	0	0	0	0
Cyprinodontidae	1	3	4	0	0	0	0	0	0
Poeciliidae	1	1	2	0	0	0	0	0	0
Gadidae	1	1	1	1	1	1	100	100	100
Percopsidae	1	1	1	1	1	1	100	100	100
Aphredoderidae	1	1	1	0	0	0	0	0	0
Serranidae	2	2	2	0	0	0	0	0	0
Percidae	11	21	26	4	4	4	36	19	15
Centrarchidae	5	12	12	1	1	1	20	8	8
Atherinidae	1	1	1	0	0	0	0	0	0
Sciaenidae	1	1	1	0	0	0	0	0	0
Cottidae	2	4	5	2	4	4	100	100	80
Gasterosteidae	3	3	3	2	2	2	67	67	67
Total	94	173	236	31	41	49	33	24	21

* As listed by Hubbs and Lagler (1947), with the addition of the three new subspecies described in this report.

† More than the one introduced species of lamprey will perhaps be found about Isle Royale on further exploration.

‡ Other species of Coregonidae will no doubt be added to the Isle Royale fauna when the deeper surrounding waters are fished.

§ Another catostomid may be indicated by the reports of "mullet" and "carp" in the commercial fishery.

tained evidence that *Stizostedion v. vitreum* had been stocked as fry, but it was no doubt a native species, since Isle Royale is well within its natural range.

The fish fauna of Isle Royale is rather depauperate (Table II), but not surprisingly so, in view of the northern latitude and the isolated position of the island in a large cold lake. No representatives are known of thirteen families that penetrate the Great Lakes basin from the south, namely, Polyodontidae, Lepisosteidae, Amiidae, Hiodontidae, Clupeidae, Ameiuridae, Anguillidae, Cyprinodontidae, Poeciliidae, Aphredoderidae, Serranidae, Atherinidae, and Sciaenidae. A few species of Polyodontidae, Hiodontidae, Ameiuridae, and Sciaenidae are known from Canada north of the Great Lakes (Dymond, 1947), but appear not to have become established about Isle Royale. The Isle Royale fauna has a poor representation of several other families that are essentially southern as related to the Great Lakes, namely, the Petromyzonidae (the one representative is a recent invader; other species may be discovered), Catostomidae, and Centrarchidae. Of the Cyprinidae that reached the Great Lakes more than one third of the genera and more than one fourth of the species have populated Isle Royale—a tribute to the ability of this group to predominate. A good showing is made by the Percidae. There is a large representation of the Salmonidae, Coregonidae, and Esocidae—essentially northern groups. The coregonids would be better accounted for had the deep waters about Isle Royale been explored. The Isle Royale fauna includes all the Great Lakes representatives of Acipenseridae, Osmeridae (introduced), Gadidae, Percopsidae, and Cottidae (except for one mainland subspecies), and two of the three species of Gasterosteidae; these six families are all of northern distribution. The lack of Umbridae on Isle Royale is attributable to the failure of *Umbra limi* to range so far north in the Great Lakes. The absence of Thymallidae is related to the highly localized distribution of grayling in the southern part of its range. In approximate figures the Isle Royale fish fauna comprises one half of the Great Lakes fauna in terms of families; one third in terms of genera; one fourth in terms of species; one fifth in terms of total kinds.

The occurrence of each species in the Isle Royale fish fauna is primarily attributable to incursion; secondarily, to survival or differentiation. Like other parts of the Great Lakes region, Isle Royale was populated during and after the melting of the last continental ice sheet (Greene, 1935; Radforth, 1944; Hubbs and Lagler, 1947). Recession of the Wisconsin glacier opened channels for the reinvasion of the waters of Lake Superior by the fishes that had survived in nonglaciated areas in Alaska and in the upper Mississippi Valley and probably also in meltwater around the margins of the glacial lobes. From the northwest or from the meltwater, perhaps from both sources, probably came such northern types as: the Salmonidae, other than the introduced rainbow trout; the Coregonidae; possibly the Esocidae (*Esox lucius* and *Esox m.*

masquinongy); the Gadidae (*Lota lota maculosa*); the Cottidae; and one of the Gasterosteidae, namely, *Pungitius pungitius*.

Some of these species may also have reinvaded the Great Lakes from the upper Mississippi Pleistocene refuge (the Driftless Area). All species other than those listed above, except, of course, the three that have spread to Isle Royale in modern times, presumably reached the Great Lakes and ultimately the island from the Mississippi basin, through one of the several glacial outlets and thence through the glacial Great Lakes. They are among the species which are supposed to have reinvaded the Great Lakes through most or all of the main outlets, after which they dispersed widely through the Great Lakes basin.

As Ruthven (1909 : 329) remarked, it is difficult to understand how some of the species that now occur in the lakes and streams of Isle Royale reached such habitats from any other favorable waters; how certain of the weaker fishes and certain of the pond types could ever have swum across the wide, deep channel of almost icy water that separates Isle Royale from the adjacent mainland shore, which in itself is not particularly favorable to such fishes. As Koelz put it, in his manuscript report: "A journey of twenty-five miles across a depth largely over 600 feet, in water that for most of the year is near freezing, is hardly to be expected from fish that do not regularly grow larger than three inches and prefer to live on warm shoals." The Isle Royale species that we have in mind in this connection are those that were seldom or never collected around the Lake Superior shore and those that are not represented in Lake Superior by closely related types. These are: *Semotilus a. atromaculatus, Margariscus margarita* (two subspecies), *Pfrille neogaea, Chrosomus eos, Notemigonus crysoleucas auratus, Notropis heterodon, Notropis v. volucellus, Notropis heterolepis* (two subspecies), *Pimephales promelas* (two subspecies), *Percina caprodes semifasciata, Poecilichthys exilis, Lepomis gibbosus,* and *Eucalia inconstans* (which occurred in one shore collection, obviously as a straggler).

Several theories might be advanced to explain how such fishes reached Isle Royale:

(1) They may have been brought to the island by some such fortuitous means as the transport of eggs or of some other stage by birds or by high winds, with or without the aid of rafts. Such an idea seems inherently improbable, though it is strengthened by the circumstances that *Semotilus a. atromaculatus* and *Notropis heterodon* were each taken at

only one place and that several other species seem to be restricted to a small part of the island. Thus *Poecilichthys exilis* has been taken only in Chickenbone and Sargent lakes, both tributary to McCargoe Cove, and *Percina caprodes semifasciata* is known only from Lake Siskiwit and its outlet and from Lake Whittesey and Dustin Lake not far distant.

(2) They may have followed smaller watercourses on a land bridge or on the Lake Superior bottom when and if it was exposed during the evolution of the present Great Lakes. Such a route of incursion was favored by Koelz, but the survey of the Pleistocene geology of the island by George Stanley in 1930 leaves no reason to believe that any fish could have reached the island by any means other than swimming from the mainland across the intervening channel, no matter how wide, deep, and cold it may have been. There is no evidence of any postglacial land connection between Isle Royale and the mainland. Had such a connection existed it would probably have made possible the invasion of the island by *Cottus b. bairdii* and perhaps by other creek fishes.

(3) They may have, or have had, greater powers of dispersal across cold deep waters than is generally recognized. There is some evidence that waters ecologically unsuited to a species may serve as a channel of dispersal rather than as a barrier. For example, the open waters of Lake Michigan were found by Hubbs (unpublished notes, 1917–20) to be the probable route by which small-stream fishes reached creeks north of Chicago that flow in V-shaped valleys and that obviously were never connected with any body of water other than Lake Michigan. Such fishes would not be expected to inhabit the waters of Lake Michigan, and none were disclosed there by seining or by observation until huge fish populations, killed by bad water conditions, were washed ashore in windrows. Then a few examples of each of the creek species were found to have been living in the lake. Such ecological misfits would undoubtedly have entered any small creek that they encountered. Similarly, any pond or creek fish that became lost in the unfavorable waters of Lake Superior might have wandered widely, and a few might have reached Isle Royale. Perhaps some that were washed into the lake during floods accompanied brush that floated to the island. Since any fish in the latitude of Isle Royale are forced to live in icy water for several months each winter, their ability to survive for a considerable time in Lake Superior is to be expected. Crossings from the mainland may have been very rare events — as is typical in the populating of an island by any kind of animal — but thousands of years have elapsed since the Lake

Superior basin became filled with water in place of ice. The occurrence in Lake Superior and in immediately adjacent lowland waters of thirty-eight kinds of fish (more than 70 per cent of the island fauna) argues for the ability of fishes to live in the big lake.

(4) During a warm postglacial period, such as has been postulated on the basis of pollen studies, Lake Superior may have interposed a less formidable barrier against the invasion of fishes from the mainland. The occurrence of warm-water relicts in the north, as in Wisconsin (Greene, 1935) and in the northern parts of the mainland of Michigan, strongly suggests that southern types temporarily became much more widely dispersed to the north than they are at present. To us it seems highly plausible that some of the fishes listed on page 84 may be warm-water postglacial relicts in the interior waters of Isle Royale. Perhaps some of the fishes that occur also around the marginal shores reached the island at a time when Lake Superior became much warmer for a longer part of the year.

Although Lake Superior has served as a passageway from the mainland to Isle Royale even for creek and pond fishes, it apparently has been a barrier to a few others—or, these species, having once crossed, did not find in Isle Royale conditions favorable enough to effect their perpetuation. Of the thirty-six kinds of fish reported by Smith and Moyle (1944 : 115–124) from the Lake Superior tributaries along the Minnesota north shore, the only ones that have not become established on Isle Royale are: *Salmo trutta fario* (introduced); *Rhinichthys atratulus meleagris* (creek fish, locally abundant here, at northern end of range); *Notropis cornutus frontalis* (common stream fish, but near northern end of range); *Hybognathus hankinsoni* (uncommon; a bog-water species at northern end of range); *Bolesoma n. nigrum* (a small fish of sand bottoms, not likely to wander far in open water); *Micropterus d. dolomieu* (probably introduced); *Lepomis m. macrochirus* (possibly introduced); and *Cottus b. bairdii* (the stream form, less likely than *C. b. kumlieni* to negotiate the barrier).

Fishes which occur along the Canadian north shore of Lake Superior or on both sides of that region, but which apparently have not attained Isle Royale waters, are indicated, from the distributional data given by Radforth (1944) and by Dymond (1947), to be: *Salmo trutta fario*;[2] *Moxostoma aureolum* and *M. anisurum* (these may be the fishes that were commercially listed as "mullet" and "carp" from Isle Royale); *Notropis cornutus frontalis*;[2] *Hyborhynchus notatus* (a small, rather inactive bottom dweller); *Stizostedion c. canadense* (of spotted distribution in the north); *Bolesoma n. nigrum*;[2] *Micropterus d. dolomieu* (of restricted occurrence as a native fish in the northern end of its range); possibly also the largemouth bass, *Micropterus salmoides; Ambloplites r. rupestris; Cottus b. bairdii.*[2]

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[2] For comments see list in preceding paragraph. In these lists we disregard the deep-water coregonids that have not been sampled on Isle Royale.

Considering the data for Lake Nipigon (Dymond, 1926) and Nipigon River we add to this list only one coregonid, *Leucichthys nipigon,* which is restricted to Canadian lakes.

It is obvious that the sparsity of kinds of fish on Isle Royale is attributable much more to the very limited fauna of the adjacent shores of Lake Superior than to the barrier of cold deep water. Most of the species that have come within reasonable reach of Isle Royale have somehow been able to cross this barrier and have survived on the island, at least locally. The species that appear not to have traversed the channel are of either rare or local occurrence so far north or appear to have been relatively recent arrivals from the south. They may not have had time to disperse to the island or may have arrived subsequent to the warm postglacial period, when the barrier was less effective.

It is improbable that all fish immigrants to Isle Royale have survived. It may be assumed that there has been at least local extirpation, particularly of the cold-water, clear-water pioneers. Thus most of the inland lakes were no doubt at first occupied by coregonids, which have vanished in all but the four largest and deepest lakes (p. 95). Two species, *Cristivomer namaycush* and *Catostomus c. catostomus,* though now absent, were in all probability originally present in the higher lakes of Isle Royale, for they occur, as relatively very ancient relicts, above falls in the higher lakes of the Huron Mountains on the south shore of Lake Superior (Hubbs, 1929). The occurrence of *C. c. commersonnii* in the higher lakes of Isle Royale but of *C. c. catostomus* in those of the Huron Mountains may reflect a strong competition between these species of suckers where living in restricted waters. Two other species that occur in the Huron Mountain lakes, namely, *Salvelinus fontinalis* and *Couesius p. plumbeus,* have each survived in only one of the higher lakes on Isle Royale.

At comparably high levels above Lake Superior, however, the fish fauna of the Isle Royale lakes is richer and more varied than is that of the Huron Mountain lakes (Table III) and comprises a number of spe-

TABLE III

DISTRIBUTION OF FISHES IN HIGH LAKES OF ISLE ROYALE AND ON THE SOUTH SHORE OF LAKE SUPERIOR

Region	ISLE ROYALE			HURON MTS.			PORCUPINE MTS.	
Lake	Others	Desor	Lily	Ives	Others	Cliff	Carp†	Little Carp‡
Present elevation of lakes above Lake Superior	100′–200′	235′	400′	153′	233′–243′	315′	500′	950′
Estimated elevation of lakes above Minong Beach*	−40′–+60′	120′	300′	173′	253′–263′	335′	580′	1030′
Leucichthys artedi, subspecies	..	+	..	..	..	..	..	+
Leucichthys artedi annensis	..	..	..	..	+	..	..	..
Leucichthys artedi clemensi	..	..	..	+	+	..	..	..
Leucichthys hubbsi	..	..	..	+	..	..	..	..
Coregonus clupeaformis dustini	..	+	..	..	..	..	..	..
Salvelinus f. fontinalis	+	+	..	..	+	..	..	..
Salvelinus fontinalis, subspecies	..	..	..	..	..	..	..	+
Cristivomer n. namaycush	..	..	..	+	+	..	..	..
Catostomus c. commersonnii	+	+	..	..	..	..	+	+
Catostomus c. catostomus	..	..	..	+	+	..	..	..
Semotilus a. atromaculatus	+	..	..	..	..	..	+	+
Margariscus margarita nachtriebi	+	+	..	..	..	..	+	?
Margariscus margarita koelzi	+	..	..	..	..	..	..	..
Couesius plumbeus plumbeus	..	+	..	+	+	..	..	?
Rhinichthys atratulus meleagris	..	..	..	..	..	..	+	+
Pfrille neogaea	+	..	+	..	..	..	..	..
Chrosomus eos	..	..	..	..	..	..	+	+
Notropis cornutus frontalis	..	..	..	..	..	..	..	?
Notropis h. hudsonius	..	..	..	..	..	..	+	..
Notropis h. heterolepis	+	..	..	..	..	..	+	..
Notropis h. regalis	+	..	..	..	..	..	..	..
Pimephales p. promelas	+	..	+	..	..	..	+	+
Pimephales p. harveyensis	+	..	..	..	..	..	..	..
Hyborhynchus notatus	..	..	..	..	+	..	..	..
Esox lucius	+	..	..	..	..	..	..	..
Percopsis omiscomaycus	+	+	..	..	..	..	+	..
Perca flavescens	+	..	..	+	+	..	+	..
Cottus ricei	..	+	..	..	..	..	..	..
Cottus cognatus gracilis	..	+	..	..	..	..	..	..
Eucalia inconstans	+	+	+	..	+	..	..	+
Pungitius pungitius	+	+	..	..	..	..	..	+
Total no. of species	15	11	3	6	9	0	10	8, 9 or 10

* From George Stanley's estimates; the Minong water plane, extrapolated from positions known on Isle Royale and on the Keweenaw Peninsula, lies from 10 to 80 feet below Lake Superior near the Porcupine Mountains, and from 20 feet above to 20 below the lake near the Huron Mountains.

† Data from Ruthven (1906: 107–108) and from the Michigan Institute for Fisheries Research (1938, 1945). *Micropterus d. dolomieu* and *Lepomis m. macrochirus* have been stocked in the lake (1935, 1936). Carp Lake is now called Lake of the Clouds.

‡ Data from Ruthven (1906: 107–108) and from surveys by the Institute for Fisheries Research, August 29–30, 1941, and summer and fall of 1947. Included are a few species reported by Ruthven from Little Carp River just above the lake. Little Carp Lake is now often called Mirror Lake. Ruthven's record of *Couesius plumbeus* from Little Carp River is questioned because it is thought very possible that it was based on *Margariscus margarita nachtriebi*, with which *Couesius p. plumbeus* was confused (Hankinson, 1917). The pertinent specimens appear to be no longer extant. Nor could the specimens identified as *Nototropis cornutus* be found; nor is there any record of them in the catalog of the University of Michigan Museum.

TABLE IV

DISTRIBUTIONAL SYNOPSIS OF FISHES IN ISLE ROYALE LAKES

Based mostly on data obtained by Walter Koelz in 1929. +, records based on specimens. *R*, presumably reliable reports.

Species	Ahmeek	Amygdaloid	Angleworm	Beaver	Benson	Chickenbone	Desor	Dustin	Epidote	Eva	Feldtmann	Forbes	George	Halloran	Harvey	Hatchet	Intermediate	John	Lesage	Lily	Linklater	Livermore	Mason	McDonald	Mud	Newt	Otter	Patterson	Richie	Sargent	Shesheeb	Sholts	Siskiwit	Stickleback	Sumner	Superior*	Theressa	Wagejo	Wallace	Whittlesey	No. of lakes per species
Petromyzon marinus	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	+	. .	. .	. .	. .	1
Acipenser fulvescens	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	+	. .	. .	. .	. .	1
Salmo gairdnerii irideus	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	+	. .	. .	. .	. .	1
Salvelinus f. fontinalis	. .	. .	. .	. .	. .	. .	+	. .	. .	. .	. .	. .	. .	. .	. .	+	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	R	. .	. .	+	. .	. .	. .	. .	4
Cristivomer n. namaycush	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	+	. .	. .	+	. .	. .	. .	. .	2
Cristivomer namaycush siscowet	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	+	. .	. .	. .	. .	1
Leucichthys artedi, subspecies	. .	. .	. .	. .	. .	. .	+	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	1
Leucichthys artedi, subspecies	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	+	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	1
Leucichthys artedi sargenti	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	+	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	1
Leucichthys artedi arcturus	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	+	. .	. .	. .	. .	1
Leucichthys bartletti	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	+	. .	. .	. .	. .	. .	. .	. .	1
Leucichthys nigripinnis cyanopterus	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	+	. .	. .	. .	. .	1
Coregonus c. clupeaformis	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	+	. .	. .	. .	. .	1
Coregonus clupeaformis, subspecies	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	+	. .	. .	. .	. .	. .	. .	. .	1
Coregonus clupeaformis dustini	. .	. .	. .	. .	. .	. .	+	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	1
Prosopium cylindraceum quadrilaterale	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	+	. .	. .	. .	. .	1
Osmerus mordax	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	+	. .	. .	. .	. .	1
Catostomus c. commersonnii	. .	. .	. .	. .	. .	+	+	+	. .	. .	+	. .	. .	. .	+	+	+	+	. .	. .	. .	. .	. .	. .	+	. .	. .	. .	+	+	. .	+	+	. .	. .	+	. .	. .	+	+	16
Catostomus c. catostomus	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	+	. .	. .	. .	. .	1
Semotilus a. atromaculatus	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	+	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	1
Margariscus margarita nachtriebi	. .	. .	. .	. .	. .	. .	+	. .	. .	. .	. .	+	. .	. .	. .	+	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	3
Margariscus margarita koelzi	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	+	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	1
Couesius p. plumbeus	. .	. .	. .	. .	. .	. .	+	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	+	. .	. .	. .	. .	2
Rhinichthys c. cataractae	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	+	. .	. .	. .	. .	1
Pfrille neogaea	. .	. .	. .	. .	+	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	+	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	+	+	. .	. .	+	. .	5
Chrosomus eos	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	+	. .	. .	+	. .	2
Notemigonus crysoleucas auratus	. .	. .	. .	+	. .	. .	. .	. .	. .	+	. .	. .	. .	+	. .	. .	+	. .	. .	. .	+	. .	+	. .	. .	. .	+	. .	+	+	+	. .	. .	. .	. .	+	. .	. .	. .	. .	11
Notropis atherinoides: acutus × atherinoides	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	+	. .	. .	+	. .	. .	. .	. .	2
Notropis h. hudsonius	. .	+	. .	+	. .	+	. .	. .	. .	+	. .	. .	. .	. .	. .	. .	+	. .	. .	. .	. .	. .	. .	. .	. .	. .	+	. .	+	+	. .	. .	+	. .	. .	+	. .	. .	. .	+	11
Notropis heterodon	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	+	. .	. .	. .	. .	1
Notropis v. volucellus	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	+	. .	. .	. .	. .	. .	. .	+	. .	. .	. .	. .	2
Notropis h. heterolepis	. .	. .	. .	+	+	. .	. .	+	. .	+	. .	+	. .	+	. .	. .	+	+	. .	. .	+	+	+	. .	+	. .	+	. .	+	+	+	+	+	. .	+	+	+	. .	+	. .	22
Notropis heterolepis regalis	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	+	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	1
Pimephales p. promelas	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	+	. .	. .	. .	+	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	+	+	. .	. .	+	. .	5
Pimephales promelas harveyensis	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	+	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	1
Esox lucius	+	+	+	+	R	+	. .	+	+	+	+	. .	+	+	. .	. .	+	+	+	. .	+	+	+	+	+	. .	+	+	+	+	+	+	+	. .	. .	+	. .	+	. .	+	30
Esox m. masquinongy	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	+	. .	. .	. .	. .	1
Lota lota maculosa	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	+	. .	. .	+	. .	. .	. .	. .	2
Percopsis omiscomaycus	. .	. .	. .	. .	. .	. .	+	. .	. .	. .	. .	. .	. .	. .	. .	+	+	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	+	. .	. .	. .	+	. .	. .	+	. .	. .	. .	+	7
Perca flavescens	+	+	+	+	+	+	. .	+	+	. .	+	+	+	+	+	. .	+	+	+	. .	+	+	+	+	. .	. .	+	+	+	+	+	+	+	. .	. .	+	. .	. .	. .	+	29
Stizostedion v. vitreum	. .	. .	. .	. .	. .	+	. .	+	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	+	. .	. .	. .	+	4
Percina caprodes semifasciata	. .	. .	. .	. .	. .	. .	. .	+	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	+	. .	. .	+	. .	. .	. .	+	4
Poecilichthys exilis	. .	. .	. .	. .	. .	+	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	+	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	2
Lepomis gibbosus	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	+	. .	. .	. .	. .	. .	+	. .	. .	. .	. .	. .	. .	+	. .	. .	. .	. .	3
Triglopsis thompsonii	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	+	. .	. .	. .	. .	1
Cottus ricei	. .	. .	. .	. .	. .	. .	+	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	+	. .	. .	+	. .	. .	. .	+	4
Cottus bairdii kumlieni	. .	. .	. .	. .	. .	+	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	+	. .	. .	. .	. .	2
Cottus cognatus gracilis	. .	. .	. .	. .	. .	+	+	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	+	. .	. .	. .	. .	. .	+	+	. .	. .	+	. .	. .	+	. .	. .	. .	. .	7
Eucalia inconstans	. .	. .	. .	. .	. .	. .	+	. .	. .	. .	. .	. .	. .	. .	+	+	. .	. .	. .	+	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	+	+	+	+	+	. .	+	. .	10
Pungitius pungitius	. .	. .	. .	. .	. .	. .	+	. .	. .	. .	. .	. .	. .	. .	. .	+	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	+	. .	. .	+	. .	. .	. .	. .	4
Number of kinds per lake†	2	3	2	5	4	8	11	6	2	4	3	3	2	4	6	8	7	4	2	3	4	3	6	2	3	0	5	2	11	9	4	4	17	1	4	38	2	1	6	8	

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* Including adjacent stream mouths, marshes, and ponds not more than twenty-five feet higher than the Lake Superior.

† The percentages of the fauna occurring in each lake are approximately twice the number of kinds.

cies that are presumed to have reëntered the Lake Superior basin later in the sequence of postglacial reinvasion. This difference may be attributed to two causes.

In the first place, after the Isle Royale lakes had been formed by the receding levels of the glacial Great Lakes, fishes were less abruptly and less completely isolated. The outlets of the higher lakes on the island are not blocked by such impassable barriers as exist in the outlets of all higher Huron Mountain lakes other than Trout (Hubbs, 1929). At present most of the outlets on Isle Royale are too small to serve effectively as channels by which fishes can ascend to the lakes, but during some moister postglacial period there was presumably a more ample discharge.

In the second place, the Isle Royale lakes were cut off from the antecedent of Lake Superior at a later time than were the Huron Mountain lakes. They are now, it is true, about as high above Lake Superior, but this elevation is due in large part to tilting of the land surface during the postglacial isostatic readjustment. The relative age of the lakes is indicated much better by their height above the Minong water plane than by their present elevation above Lake Superior (Table III). The Minong beach represents a lake stage intermediate between Lake Algonquin and Lake Nipissing. On Isle Royale, according to George Stanley's personal communication, it grades from about 165 feet above Lake Superior in the northeastern part of the island to only 80 feet near the southwestern end. By extrapolation of Stanley's estimates the Minong level near the Huron Mountains lies from 20 feet below to 20 above present Lake Superior. Except for Lake Desor and Lily Lake the higher Isle Royale lakes lie from about 40 feet below to about 60 feet above the Minong plane, whereas the fish-containing Huron Mountain lakes are situated about 170 to 260 feet above the same plane, according to Stanley's estimates. Though Lake Desor is 235 feet above Lake Superior, it is only about 120 feet above the Minong plane and, therefore, is less ancient than the Huron Mountain lakes that are at almost exactly the same elevation above Superior. Lily Lake lies nearly 400 feet above Superior and about 300 feet above the Minong water plane.

The higher Isle Royale lakes harbor several kinds of fish that do not occur in the older, originally higher, Huron Mountain lakes, or are represented there only in Trout Lake. These forms fall into several categories:

(1) Glacial Great Lakes relicts, in Lake Desor, that are represented by cognates in the higher Huron Mountain lakes: *Leucichthys artedi,* subspecies, and *Coregonus clupeaformis,* subspecies.

(2) Species that occur in none of the higher Huron Mountain lakes and are not represented there by cognates. Included are northern types that are probably glacial Great Lakes relicts, which have become extirpated in the Huron Mountain lakes, just as other relicts have become extinct in the Isle Royale lakes (p. 87). Included also are more southern types that are presumed to have arrived in the Superior basin after the Huron Mountain lakes were cut off by barriers in the outlets. Not all the species are readily assignable to either category, but, tentatively, they may be listed in the following sequence of decreasing age as inhabitants of the Superior basin: 1, *Pungitius pungitius;* 2, *Cottus cognatus gracilis;* 3, *Cottus ricei;* 4, *Esox lucius;* 5, *Percopsis omiscomaycus;* 6, *Margariscus margarita* (two subspecies); 7, *Pfrille neogaea;* 8, *Catostomus c. commersonnii;* 9, *Notropis heterolepis* (two subspecies); 10, *Pimephales promelas* (two subspecies); 11, *Semotilus a. atromaculatus.* Toward the middle of this list the assigned sequence is particularly arbitrary.

(3) Kinds not represented in higher Huron Mountain lakes, except in Trout Lake, which has no impassable barrier in its outlet: *Salvelinus f. fontinalis* and *Eucalia inconstans.*

Lake Desor, the highest of the Isle Royale lakes, with the exception of the pond named Lily Lake, has eleven fish species, nearly twice as many as are native in any of the upper Huron Mountain lakes. Its large size and its varied habitats are the apparent reasons for the retention of early postglacial arrivals, and the gradient of its outlet seems to have permitted the entry of *Catostomus c. commersonnii, Semotilus a. atromaculatus, Margariscus margarita nachtriebi,* and *Eucalia inconstans,* if any or all of these arrived in the region after Lake Desor was formed.

The Lily Lake fauna comprises three northern bog-water fishes, *Pfrille, Pimephales,* and *Eucalia.* These may have entered by an outlet, or they may be relicts dating from the ancient origin of the lake. If they are relicts here, they probably occurred originally in the higher Huron Mountain lakes but failed to survive because of rather unfavorable conditions. At present Lily Lake lies in a shallow trough, but at an earlier, moister, period it may have risen high enough to discharge over the lowest point in the surrounding rim, either to the north or to the south. The pertinent physiographic evidence should be checked.

In several fish-faunal respects the higher Isle Royale lakes agree with Carp Lake (Lake of the Clouds) and Little Carp Lake (Mirror Lake), which lie high in the Porcupine Mountains (Ruthven, 1906). These high lakes on Isle Royale and in the Porcupine Mountains are inhabited by several species that do not occur in the higher waters of the Huron Mountains (Table III and Hubbs, 1929). Some may have existed there at an early date, but if so, they appear not to have survived. Others probably arrived in the Lake Superior basin after the Huron Mountain lakes were cut off. The time when the species that occur in the Porcupine Mountain lakes arrived may eventually be measured by a dating, in glacial lake terms, of the falls in the lower and mid sections of the outlet streams (Carp River and Little Carp River). This sort of study is much needed in the analysis of the past and present distribution of fishes in the Great Lakes region.

The richness of the Isle Royale fish fauna decreases with elevation (Fig. 2). The number of species in the five main elevation categories decreases as follows: 40, 20, 15, 11, 3 (the percentage composition is approximately twice the number of species). Part of this decrease is due to the fewer waters and less varied habitats at the higher reaches. Historical factors, however, are probably also prominently involved. Many of the species that are confined to the lower waters probably arrived late in the sequence of postglacial redispersal and have not been able to ascend the generally small and intermittent streams of Isle Royale to the higher lakes.

In the waters of Isle Royale the fishes are scatteringly distributed, as though chance may have played an important rôle in dispersal and survival (Table IV). Twenty-four kinds, comprising nearly half of the Isle Royale fish fauna, are not known to occur in more than one lake. Eight kinds are known to inhabit only two lakes. Combinations of four lakes make up the habitat of five forms. Further considering the number of lakes per species, we find that three lakes, five lakes, seven lakes, and eleven lakes comprise the entire known habitat of two species. Of five ubiquitous kinds, one occurs in ten lakes, one in sixteen lakes, another in twenty-two lakes, another in twenty-nine lakes, and yet another in thirty lakes. The limited habitat of many of the forms is in part accounted for by the local differentiation of several of the species.

In general, the larger as well as the lower lakes have the higher number of species. In the order of known number of kinds of fish the lakes rank as follows:

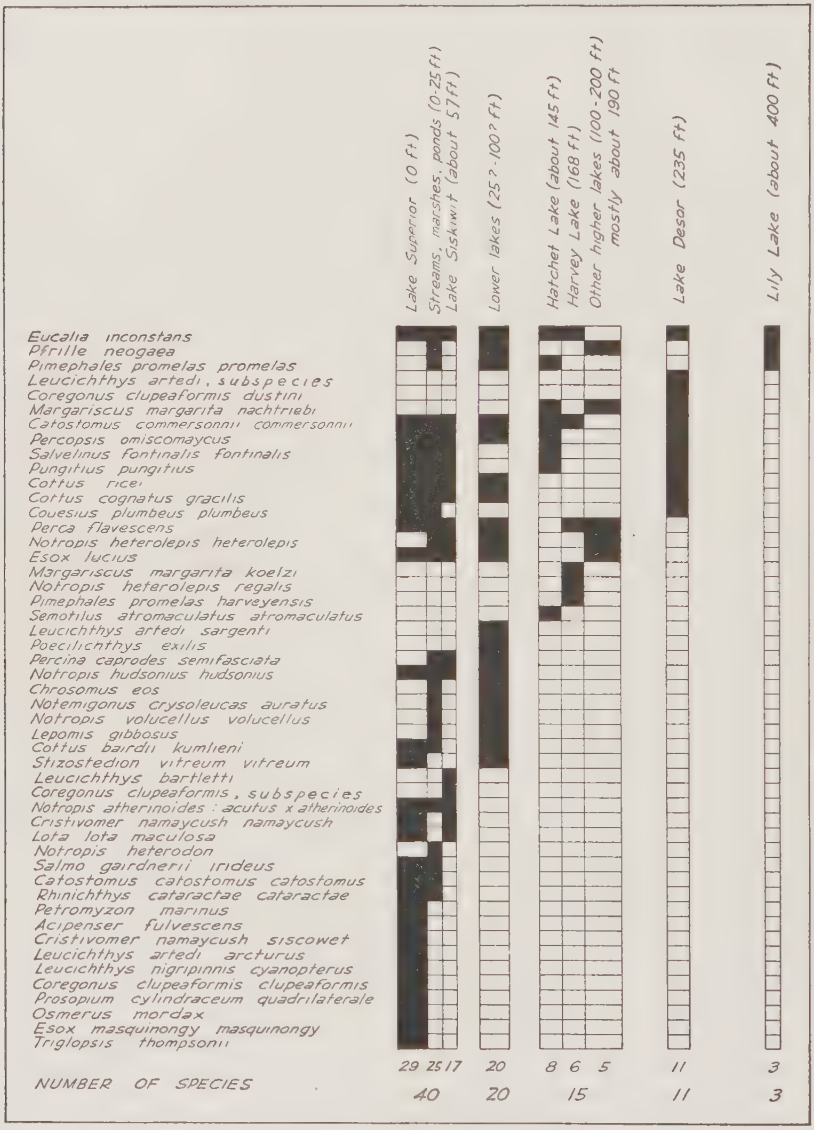

FIG. 2. Analysis of the Isle Royale fish fauna, mostly by lakes and by groups of lakes having similar elevation

Thirty-eight kinds: Lake Superior and adjacent stream mouths, ponds, and marshes less than 25 feet higher than the main lake.

Seventeen kinds: Siskiwit Lake, by far the largest of the inland lakes and one of the lower in elevation (57 feet).

Eleven kinds: Lakes Richie and Desor, next in order of size, except perhaps for Lake Feldtmann (a low-elevation but very shallow lake, in which only three species were caught). Lake Richie is one of the lower lakes (less than 100 feet elevation), but Lake Desor is the highest (235 feet) of the main lakes.

Nine kinds: Sargent Lake, next in order of size, and one of the lower lakes.

Zero to eight kinds: other inland lakes in which there seems to be very little correlation between number of species and either the size of the lake or its elevation.

ECOLOGICAL ANALYSIS OF THE FAUNA

On and about Isle Royale we recognize seven major habitat types that appear to harbor distinctive fish associations: (1) Lake Superior, from a depth of eight fathoms to the shore zone; (2) the exposed shore; (3) the stream mouths, base-level portions of streams, and sheltered, sometimes vegetated, coves; (4) the boggy streams, beaver ponds, and dystrophic lakes; (5) the rapid streams; (6) the lakes in various stages of eutrophication but not harboring coregonids; (7) the more or less oligotrophic lakes inhabited by coregonids.

Fauna of Lake Superior from a depth of eight fathoms to the shore zone. — The fishes that characteristically dwell in less than fifty feet of water during summer months, twenty kinds, are known from our experimental gill-net collections, from the commercial fish take, and from anglers' reports. They are: *Petromyzon marinus, Acipenser fulvescens, Salmo gairdnerii irideus, Salvelinus f. fontinalis, Cristivomer n. namaycush, C. n. siscowet* (perhaps chiefly in still deeper water), *Leucichthys artedi arcturus, L. nigripinnis cyanopterus* (generally in deeper water), *Coregonus c. clupeaformis, Prosopium cylindraceum quadrilaterale, Osmerus mordax* (probably), *Catostomus c. commersonnii, C. c. catostomus, Couesius p. plumbeus, Esox lucius, E. m. masquinongy* (if Ruthven's 1906 record is correct), *Lota lota maculosa, Perca flavescens, Stizostedion v. vitreum, Triglopsis thompsonii* (probably). Obviously these kinds differ in abundance and vary in numbers with the seasons. In addition to the forms cited, others, such as deep-water coregonids, may enter the habitat for spawning purposes. Some of the species listed are more characteristic of these and deeper waters than are others. For example, *Catostomus catostomus* is more typical of this portion of Lake Superior than is *C. commersonnii.*

Fauna of the exposed shore. — Another assemblage of species inhabits the rocky, often precipitous parts of the Isle Royale shore that are exposed to wave action. This habitat is not continuous around the island, but is interrupted by sheltered coves or by stretches of sharp drop-off. In practice it has been treated as the exposed hard-bottomed section of the shore zone that is seinable by wading. The most common associates are *Couesius p. plumbeus, Rhinichthys c. cataractae,* the young of the two species of *Catostomus, Percopsis omiscomaycus, Cottus bairdii kumlieni, C. cognatus gracilis,* and *Pungitius pungitius.* Other kinds occur less frequently, or are thought to occur, to bring the probable total to twenty.

Fauna of the stream mouths, base-level parts of streams, and sheltered, sometimes vegetated, coves. — Most common here are *Catostomus c. commersonnii, Couesius p. plumbeus, Rhinichthys c. cataractae, Percopsis omiscomaycus, Cottus cognatus gracilis, Eucalia inconstans,* and *Pungitius pungitius.* Other fishes inhabiting sheltered waters of this sort are strays from zones where they are more abundant. The species listed are the typical elements, but a total of about thirty-one kinds may be represented.

Fauna of the boggy streams, beaver ponds, and dystrophic lakes. — Although they range in elevation from some of the lowest bodies of water (almost base-level beaver ponds) to the highest water studied (Lily Lake), such senescent waters have fish-faunal elements in common. *Eucalia inconstans* occurs in nearly all of them. *Pfrille neogaea, Chrosomus eos,* and *Pimephales p. promelas* are, however, most characteristic elements, since on the island they are common in and are largely confined to such boggy situations. Such habitats are characteristic of these species through Michigan. The nine kinds that are represented include, in addition to the species named above, *Catostomus c. commersonnii, Notemigonus crysoleucas auratus, Notropis h. heterolepis, Esox lucius,* and *Perca flavescens.* The waters involved are all shallow, soft-bottomed, and brownish. The lakes included are those that have predominantly bog borders and are mostly not over ten feet deep, namely, Ahmeek, Wallace, Sumner, Theresa, Mud, Sholts, Stickleback, and Lily (see Table I). These lakes as well as several unnamed ponds each have six or fewer fish species — on the average fewer than do the other lakes on the island.

Fauna of the rapid streams. — The fish faunas of the more rapid parts of Washington Creek, Little Siskiwit River, tributaries of Siskiwit Lake, and other streams characteristically include *Catostomus c. commersonnii, Rhinichthys c. cataractae, Couesius p. plumbeus,* and *Cottus cognatus gracilis. Salvelinus f. fontinalis* occurs in the larger streams, named above, about twice as frequently as *Salmo gairdnerii irideus. Catostomus c. catostomus* and *Cottus ricei* were also taken in rapid water. *Eucalia inconstans* occurs in these waters, but usually selects spots where the current is slack.

Fauna of the lakes in various stages of eutrophication and not now harboring coregonids. — The most common fishes in lakes of this category are *Esox lucius, Perca flavescens, Notropis heterolepis* (two subspecies), *Catostomus c. commersonnii, Notemigonus crysoleucas auratus,* and *Notropis h. hudsonius.* The number (two to eight) of species in these lakes is intermediate between that for dystrophic lakes and that for the lakes inhabited by coregonids. Lakes of this category are the most numerous on the island. All are ten feet or more in depth. They vary in size from Feldtmann, one of the five largest lakes, to Wagejo, a small pond (Table I).

Fauna of the more or less oligotrophic lakes inhabited by coregonids. — The lakes in this class are not only larger than any of the others, the very shallow Lake Feldtmann excepted, but are also the deepest (Table I). They contain the highest number of species of fish (numbers in parentheses, taken from Table IV): Siskiwit (17), Richie (11), Desor (11), and Sargent (9). The average number of species is more than twice that for the lakes of the preceding class. In all these lakes the coregonids present are distinguishable, at least by average differences, from their Lake Superior relatives.

Speciation of the Fishes

Although the fishes of the Isle Royale lakes have been isolated for not more than 12,000 to 25,000 years — the period since the recession of the last icecap — some speciation has occurred. Most of the species exhibit no evident differentiation, but several are regarded as having become subspecifically modified in certain of the lakes, and one, *Leucichthys bartletti* of Siskiwit Lake, is interpreted as specifically distinct.

The most notable differentiation is, perhaps, that of three minnows (Cyprinidae) in Harvey Lake (Pl. I). In seeking to explain why *Margariscus margarita, Notropis heterolepis,* and *Pimephales promelas* have become so changed in this one lake as to warrant subspecific separation, whereas they have remained scarcely or much less modified in other lakes on the island, our thoughts center on isolation rather than on any peculiar ecological conditions. Harvey Lake lies 168 feet above Lake Superior near the middle of the north shore (Fig. 1), therefore well above the Minong water plane (according to the findings of George Stanley). Hence its fishes may have been isolated for about 15,000 years, for Lake Nipissing is dated back about 4,000 years and the Minong stage as 6,000 to 12,000 years still farther back (estimates by Stanley). The outlet is so small and in part so steep that it has probably been a barrier to the further invasion of the lake by minnows since the lake was formed by the lowering of the Great Lakes. The outlet (into Todd Harbor) is scarcely more than one mile long — shorter than that of other Isle Royale lakes of similar elevation (Fig. 1). So far as we know, the stream has not been completely traversed to determine whether any barriers exist that may have been totally impassable to fish. In the other lakes inhabited by the same species in unmodified form the period of isolation has been shorter; or probably less complete, on account of repeated incursions. Or in other lakes the species may have been isolated equally long, or longer, but may not have speciated. It is well recognized that time is not a precise correlate of speciation.

The physical characteristics of Harvey Lake, as observed by Koelz (1929 manuscript) and by Lagler (Pl. I), offer no explanation for the differentiation of the three minnows. It is of moderate size, being little more than one mile long and one-fourth mile wide. Like many of the other lakes it is shallow; 190 soundings by Koelz indicate that there are extensive shoal areas less than six feet deep and a maximum depth, over a broad area, of thirteen feet. As in many lakes occupied by the species in unmodified form, the bottom is mostly mud, with some sand and peat in two coves and with many snags along the shore. There are no extensive lateral marshes, and the low shoreline, with areas of broken rock and vegetation, is moderately varied by coves and by three islands. When Koelz visited the lake in 1929 the surrounding area was well timbered with birch, cedar, Norway pine, white pine, and other trees characteristic of the region (in 1936 fire destroyed these woods, and recovery was slight by 1945). Pondweeds (*Potamogeton*) grow on the bottom in some abundance to depths of about ten feet. Before the water plants became heavily browsed by moose, the vegetation was probably more abundant, as it often is in lakes that are inhabited by the minnows in question. The temperature, as expected in such a lake, is rather warm (about midday on September 1, 1929, Koelz reported a range from 25.8° C. at the surface to 20.0° C. at the thirteen-foot bottom). The water is turbid, again as expected (the thermometer disappeared from sight at three feet). The chemistry of the water has not been studied, but there is no reason to suspect any outstandingly distinctive chemical features.

More extreme yet briefer differentiation seems to be exhibited by *Leucichthys bartletti*, the specifically endemic coregonid described by Koelz (1931:368–370, pl. 39) from Siskiwit Lake. Its ancestor has not been definitely determined. Its variability is perhaps due to hybridization in the past (p. 106). Its period of isolation probably approaches 5,000 years, for Siskiwit Lake lies, as determined by Stanley (personal communication), fifty-seven feet above Lake Superior, slightly higher than the Nipissing beach. Since it inhabits deep water, the species probably has remained completely isolated. It is unlikely that either it or its ancestor penetrated into the lake through the outlet, which, moreover, has a low cascade near its source. Specific differentiation is also claimed for another inland-lake form of the genus, namely, *Leucichthys hubbsi* Koelz (1929b) of Ives Lake in the Huron Mountains, but that cisco has been isolated much longer, for Ives Lake has an impassable chutelike outlet (Hubbs, 1929) and lies far above the Minong water plane.

All other coregonids of the lakes on Isle Royale are measurably different from, though conspecific, with those of Lake Superior, from the ancestors of which they were probably derived.

The *Coregonus* of Lake Desor was distinguished by Koelz (1931: 379) on the basis of a higher average number of scales, a longer head, a larger mouth, longer pectoral fins, and a slenderer body. These differences probably arose during the time since this fish became isolated, before the Minong stage (p. 89). Koelz referred to this subspecies the race in Trout Lake, Wisconsin, but we think that the two forms are distinct enough to be treated as subspecifically different, that their resemblance is due to convergence, and that *C. c. dustini* is endemic in Lake Desor.

The *Coregonus* of Siskiwit Lake, although isolated only since Lake Nipissing time, also appears to have become subspecifically differentiated from the Lake Superior whitefish, although at present it seems impracticable to name the subspecies (pp. 106–109).

The ciscoes (*Leucichthys artedi*) of the Isle Royale lakes appear to be differentiated from one another and from those of inland lakes elsewhere, as well as from the Lake Superior form, *L. a. arcturus,* though their separation is attended with some doubt (see pp. 102–104). The only distinctively named race is *L. a. sargenti* of Sargent Lake. The Lake Richie form has been identified with it, but the condition of the specimens renders impossible its definite identification. The Siskiwit Lake "herring" has also been referred to *L. a. sargenti,* but we regard it as the young of *L. bartletti.* The cisco of Lake Desor as well as that of Chautauqua Lake, New York, was illogically identified by Koelz with *L. a. huronicus,* a local form of Rush Lake, at the base of the Huron Mountains, on the south side of Lake Superior. Like the *Coregonus clupeaformis* of Siskiwit Lake, the *Leucichthys artedi* of Lake Desor appears to represent a distinct subspecific endemic, though the granting now of a name seems unwise. In Lake Desor, though the isolation has been equally long, the *Leucichthys* seems to have changed less than the *Coregonus* has. But the differentiation of both appears to have been local. Resemblances between the end products of speciation in distant, unconnected lakes is attributable to convergence, or merely to coincidence.

Other species may have become more or less differentiated on Isle Royale. As is noted on page 127, the three inland-lake populations of *Stizostedion v. vitreum* are very peculiar in appearance and may represent local differentiates.

There are some indications that ecotypic subspecies or races of *Leucichthys artedi* and of *Cristivomer namaycush* occur along the Lake Superior shores of Isle Royale.

Conservation and Preservation of the Fish Fauna

As one of us pointed out (Hubbs, 1940), aquatic life had long been neglected in the nature-preservation policies of the national parks. A definite policy, more acceptable to preservationists, is now in force, but the pressure to build up and maintain angling in the parks is so great as to demand constant vigilance on the part of all who are concerned with the implementation of the enlightened policy. We urge that a permanent ban be placed on the introduction into Isle Royale of any exotic fishes, including exotic stocks of native game species. Trout are particularly subject to raciation. Every effort should be made to maintain the indigenous races. The depletion of the native species and races should be prevented by fishing regulations and by the maintenance of productive natural conditions in the lakes and streams. Commercial fishing also should be regulated so as to prevent depletion of native stocks.

Annotated Species List

Under each species heading that follows there is given a synopsis of the known distribution on Isle Royale, along with some notes on habitat and habits, remarks on the characters and taxonomy of certain species, and diagnoses of the three new subspecies of Cyprinidae.

The fishes collected on the island have been identified by means of the criteria that have been developed in the University of Michigan Museum of Zoology since 1920. These characters are briefly and incompletely summarized in our keys to the Great Lakes fishes (Hubbs and Lagler, 1939, 1941, 1947). The last of these treatises is followed in matters of nomenclature and sequence of species. In the Coregonidae our work is based largely on the monographs by Koelz (1929a, 1931), though we take issue with a number of his conclusions regarding the systematics of the races in the inland lakes. The taxonomy of Great Lakes fishes has been treated in the publications just cited, as well as in the annotated check-list by Hubbs (1926), with supplements by Hubbs and Greene (1928) and by Hubbs (1930).

All collections on which this report is based are deposited in the University of Michigan Museum of Zoology. The directors and fish curators of that museum have granted full use of all available material and reports.

Petromyzonidae — Lamprey Family

Petromyzon marinus Linnaeus

Sea lamprey

A recent capture indicates that the sea lamprey has finally reached Isle Royale, in the course of its rapid spread through the Great Lakes, after its entry into Lake Erie through Welland Canal (Hubbs and Pope, 1937). A 9.5-inch specimen was taken from a ten-pound lake trout off Rock Harbor on August 15, 1946, by commercial fishermen, who reported their catch and sent the lamprey to Dr. John Van Oosten. The record has been published by Creaser (1947).

ACIPENSERIDAE — STURGEON FAMILY

Acipenser fulvescens Rafinesque

Rock sturgeon

No specimens of sturgeon have been collected about Isle Royale, but Karl Gilbert reports that the species is occasionally encountered by commercial fishermen in Washington Harbor. Isle Royale is well within the natural range of the species, and it is known from other localities in Lake Superior.

SALMONIDAE — SALMON FAMILY

Salmo gairdnerii irideus Gibbons

Common rainbow trout

As a result of stocking in past years, the rainbow trout (or "steelhead," as larger lake-run individuals are often called in this region) is well established in the streams and about the shore of Isle Royale. It is particularly common in Washington (Windigo) Creek and in Washington Harbor. At the east end of this harbor it was repeatedly seen with the common brook trout (*Salvelinus f. fontinalis*) in schools of ten- to twelve-inch individuals moving along the shore in about fifteen feet of water. Commercial fishermen reported to Dr. John Van Oosten in 1927 that they occasionally caught this trout about this embayment. It provides good sport fishing in Washington Creek. The first Isle Royale specimen was collected from this stream by Captain R. E. Ellsworth on September 14, 1920. The 1945 collections are L45 : 808, 810, 816, and 819 (pp. 77–78).

The brown trout, *Salmo trutta fario* Linnaeus, is reported to have been stocked inadvertently during recent years in a few localities on Isle Royale. None have been reported as having been seen or caught since the planting, and none were secured in 1945 during the seining of the streams in which the species is presumed to have been planted. It is probable that this trout failed to become established. From the standpoint of sound national park policy it is very fortunate that this exotic species did not persist, for it might have become a serious competitor with and predator upon the indigenous fishes.

Salvelinus fontinalis fontinalis (Mitchill)

Common brook trout

The brook trout is native to Isle Royale, as it is to other Lake Superior waters. It has also been stocked, which is unfortunate, since it cannot now be assured that the local populations are strictly indigenous. It now occurs in at least two lakes, in several streams and their mouths, and in Lake Superior about the island. Particular centers of abundance were found to be the Little Siskiwit River below the falls, the shoal waters at the east end of Washington Harbor, and Washington Creek. Ruthven (1906 : 109; 1909 : 330) recorded it from this stream and harbor and, as *Cristivomer namaycush,* from Benson Brook (see below). Koelz's records are from Hatchet Lake and Lake Desor. He also indicated it as probably occurring in Siskiwit Lake, from which anglers also report it. In 1930 Stanley took specimens in Desor Creek (Lake Desor outlet), just above Todd Cove, and it occurred again in this stream in our 1945 collections. "Coasters" (lake-run brook trout) are reported from Rock Harbor in the vicinity of Mott Island. The 1945 collecting stations are L45 : 802, 810, 818, 819, 825, 834, and 852 (pp. 76–81).

Cristivomer namaycush namaycush (Walbaum)
Common lake trout

As would be expected from its northern range, the lake trout (also called "Mackinaw trout") occurs on the shoals as well as in deeper waters all around the island. Koelz obtained it also in Siskiwit Lake. Smaller individuals, about twelve to eighteen inches long, were taken in our experimental gill-nets in depths of thirty-five feet and less. The 1945 collecting stations are L45 : 801, 812, 832, 844, and 847 (pp. 76–79). Commercial fish returns, conferences with fishermen, and catch inspections indicate captures in all the principal bays and coves and about most of the named islands. Specific localities mentioned in the commercial fishermen's returns include Amygdaloid Channel, Belle Harbor, Belle Isle, Chippewa Harbor, Fisherman Home Cove, Hay Bay, Johnson Island, Little Boat Harbor, Malone Island, Rock Harbor, Siskiwit Bay, Tobin Harbor, Todd Harbor, Washington Harbor, Washington Island, and Wright Island. According to Fire Guard George Allen, lake trout were taken regularly off Blake Point, on Three Foot Shoal, and in Rock Harbor during the summer of 1945. Ruthven (1906: 109; 1909 : 330) reported the species from Washington Harbor, the north shore of the island, Rock Harbor, and off the "east" coast of the island. The fingerling (41 mm. long) from Benson Brook, identified by Ruthven as *Cristivomer namaycush,* proves on reëxamination, with the better material now available, to be a brook trout (*Salvelinus f. fontinalis*).

"Deep-sea" trolling for lake trout provides great sport for visitors to the Isle Royale National Park. This species and the whitefish comprise the bulk of the commercial fish catch of the island.

Commercial fishermen about Isle Royale, as elsewhere in the Great Lakes, make the plausible claim that in addition to the siscowet there are two kinds of lake trout in the shoal waters. An investigation of the trout races is urgently needed.

Cristivomer namaycush siscowet (Agassiz)

Siscowet lake trout

The robust and fat deep-water form of lake trout known as "siscowet" is recognized readily by commercial fishermen about the island. It is probably uncommon, however. In 1927 Dr. Van Oosten saw some trout from off Good Little Boat Harbor that he supposed to be siscowets. H. F. Johnson reported to him that catches were made about Chippewa Harbor. Scotland and Anderson accurately described the fish to Lagler and told of occasionally taking it in Amygdaloid Channel and elsewhere along the north shore.

The genetic validity of the subspecies *C. n. siscowet* has yet to be established. One argument in favor of its validity is the occurrence in Rush Lake, Huron Mountains, Michigan, of typical lake trout as well as of a dwarfed type that resembles *C. n. siscowet* in several respects but differs in not being fat (Hubbs, 1929 : 155). No such type has been found in the lakes of Isle Royale.

Coregonidae—Whitefish Family

Leucichthys artedi, subspecies

Lake Desor cisco

The cisco of Lake Desor was referred by Ruthven (1909 : 330) to *Argyrosomus artedi* and by Koelz (1931 : 318) to *Leucichthys artedi huronicus.* We regard as illogical and unjustified the identification of the race of Lake Desor, as well as that of Lake Chautauqua, New York, with a subspecies (*huronicus*), the type locality of which is Rush Lake, at the base of the Huron Mountains on the south side of Lake Superior. Examination of Koelz's own data (1931 : 311, 318, 396–400) shows that the reference of the Chautauqua population to *huronicus* was without sound foundation, and an examination of the specimens he used confirms this view. The three usable specimens from Lake Desor also look unlike the types of *huronicus* in some respects. The head is flatter on the sides and in dorsal contour, which, instead of being markedly convex and down-curved in the mouth region, is nearly straight to the more horizontal and sharper premaxillaries. The mandible is more oblique, projects more strongly, and has a more definite symphyseal knob. The head is deeper, particularly in the midsection; the depth at the vertical through the posterior border of the orbit is as long as or longer (instead of shorter) than the distance from the tip of the snout to the posterior border of the orbit. On the average the paired fins are larger, as Koelz (1931 : 399) showed for the pectoral. In view of these differences we regard the two races as distinct and do not consider the long-isolated form of Lake Desor properly referable to *L. a. huronicus*. We believe that the peculiarities of the Desor stock are an expression of isolation and endemism. It may eventually be given a separate subspecies name, but for the present we do not regard it as wise to do so. Some authors, Dymond (1943 : 213; 1947 : 8–9), for example, have gone so far as to propose that no subspecies be recognized in the *Leucichthys artedi* complex. So extreme a stand we do not care to take, although we do recognize it as possible that many of the characters used by Koelz to separate the subspecies are environmentally induced. That some of the distinctions are subject to great nonracial modification has been proved by Hile (1937). The problem calls urgently for more study and for more critical analysis.

Leucichthys artedi sargenti Koelz
Sargent Lake cisco

The local race of cisco in Sargent Lake was described by Koelz (1931 : 320), whose data indicate that on the average it has fewer scales, a deeper body, and decidedly longer paired fins than the Lake Desor race. The differences are probably due to raciation during isolation. The earlier origin of the Lake Desor stock is involved.

With more or less doubt Koelz referred to *L. a. sargenti* the inadequate samples from Siskiwit Lake and from Lake Richie. The "herring" from Siskiwit we identify (p. 105) as the young of the endemic chub *L. bartletti*. On the basis of the counts and measurements taken by Koelz, the Lake Richie cisco appears to agree fairly well with *L. a. sargenti*, but the few specimens are so small and so badly injured (all or most were from stomachs of other fishes) that the identification cannot be accepted.

Leucichthys artedi arcturus Jordan and Evermann
Lake Superior cisco

The Lake Superior cisco, locally called "herring," is caught by commercial fishermen around the entire shore of Isle Royale. It was recorded from Washington and Rock harbors by Ruthven in 1906 and 1909, respectively, as *Argyrosomus artedi.*

Hankinson (unpublished notes) identified nine young specimens about an inch and a half long from the head of Tobin Harbor, July 20, 1905, as *Leucichthys.* They probably represent *L. artedi arcturus,* as do shore-seined young in our collection (L45 : 814) from the western end of Isle Royale, in the cove opposite Thompson Island.

Experimental gill-nets set in less than fifty feet of water in July–August, 1945, took specimens in Lane Cove, McCargoe Cove, Todd Harbor, Washington Harbor, Siskiwit Bay, Chippewa Harbor, and Middle Islands Passage (Stations L45 : 797, 801, 829, 833, and 847). Some of these individuals might pass as subspecies *artedi,* but they are mostly more terete and shorter-headed.

Commercial fishing returns indicate the catching of "herring," presumably of this subspecies, about the following localities: Belle Isle, Chippewa Harbor, Fisherman Home Cove, Hay Bay, Johnson Island, Malone Island, Rock Harbor, Siskiwit Bay, and Tobin Harbor.

H. F. Johnson, fishing in Chippewa Harbor in 1927, told Dr. John Van Oosten that he believed there were two kinds of shallow-water "herring" in that vicinity, one spawning near the surface over deep water and the other, looking like a tullibee (*L. a. tullibee*), spawning on sand in shallow water. It is quite possible that there are two subspecies of *L. artedi* in Lake Superior about Isle Royale. Koelz (1929 : 500; 1931 : 352) indicated the presence, in the north-shore bays of Lake Superior, of a deep-bodied race that is different from the more terete form of the open waters. The problem posed by these suspected ecotypes of *Leucichthys artedi,* as well as by those of *Cristivomer namaycush,* demands detailed and critical study.

Leucichthys bartletti Koelz
Siskiwit Lake cisco

This cisco is known only from Siskiwit Lake, from which Koelz (1931 : 368) described it as a distinct species. From the same lake

Koelz (1931 : 321) reported a number of young ciscoes, referring them to *L. a. sargenti* with the reservation that, "On account of their being so very small, it is impossible to determine the identity of these specimens." He (p. 369) contrasted *sargenti* ("herring") and *bartletti* ("chubs") as follows: "A form of *Leucichthys artedi,* probably *sargenti,* is also found in the lake. *L. bartletti* is distinguishable from this by having a reduced number of gillrakers, a much longer snout and much less body depth. It also undoubtedly lives in much deeper water and probably grows larger."

The specimens identified as *"artedi"* were found dead on the beach or floating. Those named *bartletti* were taken in gill-nets and in fish stomachs.

A close study of this material leads to the conclusion that the specimens called *"artedi"* are merely the young of *bartletti.* Some specimens, it is true, have more gill-rakers, 40 to 42, than any of the *bartletti* counted, but several others have only 25 to 37 gill-rakers, as in that species. Although we cannot explain readily why variation is greater than would be expected on the basis of counts by Koelz (1929a : 560–561; 1931 : 387, 397, 401, 405, 412–413, 421), we do not believe that the data warrant the assumption that there are two forms of *Leucichthys* in Siskiwit Lake. The difference in the length of the snout is an average one only; as measured from the anterior rim of the orbit to the tip of the premaxillaries, the snout length enters the head length 2.7 to 3.2 times in the young (*"artedi"*) and 2.5 to 2.8 times in the adult. Some of the larger of the young have the snout quite as long and the head quite as slender and rakish as in types of *bartletti.* In the young of true *L. a. sargenti* the snout is only one fifth as long as the head. In the length and form of the mandible also these young ciscoes from Siskiwit Lake agree with *bartletti* rather than with *sargenti;* the mandible is slightly more instead of decidedly less than half as long as the head, and it is slenderer, distinctly projecting, and somewhat hooked upward at its tip. Many of the young are quite as slender as the adults. The differences noted in size and habitat are, of course, merely an index of age. The scale rows, as counted in about a dozen of the young specimens, range from 62 to 76. This is not an unusual amount of variation for a cisco (see counts by Koelz, 1929a : 562–563; 1931 : 388, 398, 402, 411, 414–416).

It is therefore concluded that there is only one form of *Leucichthys* in Siskiwit Lake. With what Great Lakes species this form is allied can hardly be guessed at now. It is not at all impossible that it, like most of the inland forms, is a representative of *L. artedi* that through convergence has come to resemble the deep-water species of the Great Lakes. Whatever its origin may have been, its specific differentiation since about the time of Lake Nipissing, thus in a period of about 5,000 years, is remarkable.

Another strong possibility is that the characteristics of the Siskiwit Lake cisco are in part due to the introgression of one character, high gill-raker number, through the past hybridization of *L. artedi* with a deep-water form, followed by inbreeding. Such a speciational situation, involving a markedly skew distribution of gill-raker counts, is evident in the cyprinid genus *Siphateles* in Nevada (Hubbs and Miller, MS). A parallel case, involving scute numbers, has been demonstrated by Heuts (1947: 43–48) for *Gasterosteus*. That hybridization does occur in nature between genera of Coregonidae is demonstrated by data given by Koelz (1929a: 539–541). Furthermore, on strong circumstantial evidence, certain specimens from Lake Superior have been interpreted (Hubbs, unpublished notes) as hybrids between *Leucichthys artedi arcturus* and *L. kiyi kiyi*. A thoroughgoing analysis of the Siskiwit Lake cisco is called for.

Leucichthys nigripinnis cyanopterus Jordan and Evermann

Bluefin

This usually deep-water form, the Lake Superior representative of the "blackfin," was reported for Rock Harbor by Ruthven (1909 : 330) under the name then current, *Argyrosomus nigripinnis*.

H. F. Johnson, who has fished commercially about Chippewa Harbor since 1904, told Dr. John Van Oosten in 1927 that "blackfins" were taken in abundance in 1904, almost disappeared in 1905, and were caught in small numbers from then until 1927.

Occasional returns or reports given in the commercial fish statistics for "chubs" or "longjaws" from Chippewa Harbor and Washington Harbor may apply to this species. Such returns, however, do not distinguish between the deep-water species of coregonids, and there is little reason to doubt that some or all of the four other deep-water ciscoes of Lake Superior (see Koelz, 1929a) occur about Isle Royale. These species are shortjaw chub, *L. zenithicus*, Superior shortnose chub, *L. reighardi dymondi*, Michigan kiyi, *L. k. kiyi*, and Great Lakes bloater, *L. hoyi*. The last-named species was probably the "bloater" that Mr.

Johnson reported to Dr. Van Oosten as occasionally being caught in herring nets at Chippewa Harbor.

Coregonus clupeaformis clupeaformis Mitchill
Great Lakes whitefish

The Great Lakes whitefish is common all around the island. Young were seined on the shore, and half-grown individuals were taken in experimental gill-nets set at depths less than fifty feet. The 1945 collecting stations are L45 : 797, 801, 805, 812, 814, 816, 821, 830, 835, 844, and 847 (pp. 76–79). Commercial nets take larger specimens. Fishermen reported catches at Belle Isle, Chippewa Harbor, Rock Harbor, Siskiwit Bay, Tobin Harbor, Washington Harbor, Washington Island, and Wright Island.

Hankinson (unpublished notes) identified as of this species a young individual 1.75 inches long taken on July 20, 1905, at the head of Tobin Harbor.

The whitefish shares with the lake trout the position of greatest importance in the local commercial fishery. Some "jumbos," large individuals weighing more than four pounds, are still taken, but, according to the comments of fishermen, not so commonly as formerly.

Coregonus clupeaformis, subspecies
Siskiwit Lake whitefish

Koelz (1931 : 377) found a whitefish to be common in Lake Siskiwit. It is a rather slender form, especially in the head, and superficially somewhat resembles the Menominee whitefish, *Prosopium.* This resemblance we presume to be the basis of Ruthven's record (1909 : 330) of "*Coregonus quadrilateralis*" from Siskiwit Lake, for neither Koelz nor we took the Menominee in this body of water.

Whether the Lake Siskiwit whitefish is genetically distinct and if so, whether it warrants subspecific separation, are questions that call for consideration, although in the present state of coregonid systematics we can hardly expect to arrive at a final decision. It was identified by Koelz (1931 : 377) as *C. c. neo-hantoniensis,* with the reservation that it seems to have a slightly longer maxillary. But this identification is to be questioned, for the subspecies has been attributed to inland lakes in general, between the populations of which no genetic connection can be assumed. Furthermore, there is serious doubt regarding the validity of the chief diagnostic feature attributed by Koelz to *neo-hantoniensis*, namely, the greater length of the paired fins. On the basis of the long pectorals Koelz (1931 : 375, 428) identified as *C. c. neo-hantoniensis* the whitefish of St. Mary's Lake, Glacier National Park, in which the Great Lakes whitefish (*C. c. clupeaformis* or *C. c. latus*) had been stocked (Schultz, 1941 : 40). The population sampled may or may not have been the result of the stocking. Furthermore, runt brook trout (*Salvelinus f. fontinalis*) in cold creeks have very large paired fins. So do poeciliid fishes when stunted in aquaria. The character certainly is subject to environmental influence, and as expressed in *Coregonus clupeaformis* may have no genetic basis.

In one character, presumably of genetic significance, the Siskiwit Lake whitefish does seem to have differentiated racially from the Lake Superior form. The average number of gill-rakers is markedly reduced (Table V).

TABLE V

NUMBER OF GILL-RAKERS IN WHITEFISH (COREGONUS CLUPEAFORMIS) FROM LAKE SUPERIOR AND FROM SISKIWIT LAKE

The data for Lake Superior are from Koelz (1929a: 560), and those for Siskiwit Lake are from Koelz (1931: 425).

	Number of gill-rakers (total on first arch)						N	M	SE	$\frac{M_1-M_2}{\sqrt{SE_1^2+SE_2^2}}$
	25	26	27	28	29	30				
Superior	2	24	34	32	15	2	109	27.37	±.14	9
Siskiwit	13	8	4	..	..	..	25	25.64	±.14	
Superior	26 (24%)		83 (76 %)				..	..	..	..
Siskiwit	21 (84%)		4 (16 %)				..	..	..	..

The difference between the counts is reliable statistically. On the basis of the "percentage identifiable" it would seemingly be possible to separate the Superior and Siskiwit races subspecifically if only these were known, for more than three fourths of the specimens of each form are separable on gill-raker counts alone, when we place the dividing line so as to maximize the difference (see lower part of Table V). But the data published by Koelz (1929a, 1931) indicate such a maze of local forms that subspecific separation at present appears impracticable. The differentiation of the Siskiwit Lake whitefish from that of Lake Superior can, nevertheless, be regarded as having reached the subspecies level.

Coregonus clupeaformis dustini Koelz
Lake Desor whitefish

Koelz (1931 : 379) described this very peculiar type of whitefish from Lake Desor, where he found it to abound. He also referred to this subspecies the whitefish of Trout Lake, northern Wisconsin, but noted some difference between the specimens from the two lakes. It is presumed that the resemblances are due to convergence and that the form in Lake Desor is endemic, the product of local speciation. According to Koelz's own figures (his Table XXXIX, p. 427), the Trout Lake *Coregonus* does not have the increased scale number, a prime distinguishing feature of *dustini*. The difference in scale count is probably of the subspecies level. If we assume that the count for Trout Lake is 86 or fewer and that for Lake Desor 87 or more, we find the percentage typical (i.e. the percentage identifiable) to be 79 per cent for Trout Lake and 87 per cent for Lake Desor. On the identical basis we can separate 87 per cent of the Desor fish from 86 per cent of the Lake Superior population, as indicated by the counts of Koelz (1929a : 562–563).

The large mouth and slender form of this endemic whitefish may well be adaptations to its fish-eating habits, enforced by the paucity of normal whitefish food in Lake Desor.

Prosopium cylindraceum quadrilaterale (Richardson)
Round whitefish

The round whitefish, locally known also as the "pilot" or "Menominee," occurs all around the island. As explained above (p. 107), however, it seems probable that the one previously published record of this species from Isle Royale (for Siskiwit Lake) was based on *Coregonus clupeaformis,* subspecies. We have taken young in shore seining and half-grown and adults in experimental gill-nets set in water less than fifty feet deep at stations L45 : 797, 801, 812, 814, 816, 829, 830, 844 (report), and 847 (pp. 76–79). It is reported from Good Small Boat Harbor (Van Oosten), vicinity of Gull Rocks (Scotland and Anderson), and Rock Harbor (Baggley and Allen). The commercial fish records show catches about Rock Harbor, Siskiwit Bay, and Wright Island.

OSMERIDAE — SMELT FAMILY

Osmerus mordax (Mitchill)

American smelt

Young smelt were abundant in the shallows of the west end of Siskiwit Bay about the mouth of the Big Siskiwit River on July 26, 1945, when they were seined in darkness from 10:15 to 11:15 P.M. (L45 : 830). It seems probable that spawning runs have become established in this river. The occurrence of this cold-water fish on Isle Royale is evidence of its ability to traverse considerable stretches of open water. Not indigenous to the Great Lakes, the species was introduced at various times from 1912 through 1921 into Michigan waters. In 1932 the westernmost record in Lake Superior was for Keweenaw Bay (Van Oosten, 1937). Raymond E. Johnson, of the Minnesota Department of Conservation, tells us that the smelt was reported from Minnesota's north shore of Lake Superior by commercial fishermen in 1945 and was taken in the spring of 1946 at the mouth of the French River and from the St. Louis River. The species has thus about completed its spread through the Great Lakes.

CATOSTOMIDAE — SUCKER FAMILY

Catostomus commersonnii commersonnii (Lacépède)

Common white sucker

In contrast to *Catostomus c. catostomus,* which is most abundant in the waters margining the island and which lives inland in only a few streams, *C. c. commersonnii* occurs extensively in streams and their mouths and in many inland lakes, as well as about the shore and in the shallower waters of Lake Superior. It was taken by Koelz in fifteen inland lakes (Table IV) and by Lagler during the 1945 survey at stations L45 : 798, 800, 801, 803, 808, 809, 811 to 814, 816, 819 to 822, 826, 829, 830, 837, 838, 840, 841, 843, 846, 850, and 851 (pp. 76–81). This sucker was reported by Ruthven (1906 : 109; 1909 : 330) from Washington and Rock harbors. Captain Ellsworth collected specimens in the mouth of Washington River and in McCargoe Cove. Stanley took it in Pickerel Cove, a feeder to Lake Desor, Siskiwit Lake, mouth of

Little Siskiwit River, and outlet of Lake Shesheeb. Commercial fish returns list "white suckers" from Washington Harbor and Washington Island. Single entries in these records and verbal reports of fishermen in 1945 for an occasional "mullet" or "carp" may refer either to the common white sucker or to some species of redhorse (*Moxostoma*).

Catostomus catostomus catostomus (Forster)
Eastern sturgeon sucker

This sucker occurs principally in waters margining the island. The young are most common about the shore, and the subadults and adults frequent the shallower offshore zones. Collections were obtained in 1945 at stations L45 : 797, 798, 800, 801, 805, 809, 811, 812, 814, 816, 819 to 821, 829, 830, 841, 844, and 847 (pp. 76–79). Previously Captain Ellsworth had taken one in McCargoe Cove, and commercial fish returns indicated its presence at Washington Harbor. The species occurs only sparingly in the streams of the island and, so far as known, not at all in the inland lakes — a remarkable circumstance, considering the distribution of the species in other waters about Lake Superior (Hubbs, 1929). It was presumably originally present in the higher inland lakes but has not survived in them (p. 87). Its local distribution is largely complementary to that of the common white sucker (*Catostomus c. commersonnii*). Both kinds, however, spawn in the streams. One male collected on July 21 (at station L45 : 812) had milt running.

CYPRINIDAE — MINNOW FAMILY

Semotilus atromaculatus atromaculatus (Mitchill)
Northern creek chub

The only locality where this species is known on Isle Royale is Hatchet Lake, where Koelz took very large specimens. This isolated record is surprising. Were it not for the remoteness of Isle Royale one might attribute the occurrence to the escape of bait minnows. That the species was a rather early postglacial migrant and could be native in Hatchet Lake is attested by its abundance in the high lakes of the Porcupine Mountains on the south side of Lake Michigan, above falls in the lower courses of the outlet streams (Ruthven, 1906 : 107), and by its widespread occurrence in the north-shore tributaries of Lake Superior in Minnesota (Smith and Moyle, 1944 : 120).

Margariscus margarita nachtriebi (Cox)

Northern pearl dace

(Pl. II, Fig. 2)

This dace was taken by Koelz in Hatchet, Desor, and Forbes lakes. On the island it is apparently restricted to these bodies of water, for it has not been found elsewhere during the extensive collecting. The specimens from these three well-separated lakes appear to be typical of this widely spread northern subspecies. Only those from Forbes Lake approach the endemic subspecies of Harvey Lake. *Margariscus m. nachtriebi* ranges northward through most of Canada south of the tundra (Dymond, 1926 : 46; 1947 : 19).

Margariscus margarita ***koelzi,*** new subspecies

Harvey Lake pearl dace

(Pl. II, Fig. 1)

In Harvey Lake *Margariscus margarita,* like *Pimephales promelas* and *Notropis heterolepis,* is represented by an endemic subspecies.

Type specimens.—The holotype, an adult specimen 84 mm. in standard length, was collected by Walter Koelz on the shoals of Harvey Lake, Isle Royale, on September 1, 1929. It is deposited in the University of Michigan Museum of Zoology (Cat. No. 100010). The paratypes comprise thirty-five specimens, 43 to 82 mm. long (U.M.M.Z., No. 100011), collected with the holotype, and twelve examples, 22 to 101 mm. long (U.M.M.Z., 144473), collected by Karl F. Lagler and his party at station L45 : 813, in the same lake about the source of the outlet, July 21, 1945 (Pl. I, Fig. 3).

Diagnosis.—Like *M. m. nachtriebi,* but head slenderer and more conic, lips thinner, and gape less curved.

The slenderer and more conic head of *M. m. koelzi* is illustrated on Plate II, which compares the holotype of this species with a specimen of *M. m. nachtriebi* of like size from Lake Desor. The slenderness of the head is a rather consistent character (Table VI). The specimens from Hatchet Lake and Lake Desor are typical of *M. m. nachtriebi,* but those from Forbes Lake are intermediate, though probably closer to *nachtriebi* than to *koelzi.* Samples from various places in the wide range of the northern subspecies (*nachtriebi*) in general contrast sharply with *koelzi* in this character. The outstanding exception is furnished by a series of specimens collected by Walter Koelz on August 2, 1922, in a small lake

TABLE VI

RELATIVE HEAD DEPTH IN NORTHERN SUBSPECIES OF MARGARISCUS MARGARITA

As here used, the relative head depth is the distance from the occiput to the isthmus, expressed as hundredths of the head length to the margin of the opercular membrane. The measurements were made with precision calipers. The averages were computed from the uncombined data expressed in thousandths of the head length.

Subspecies and locality	Relative head depth											
	57–58	59–60	61–62	63–64	65–66	67–68	69–70	71–73	N	M	57–62	63–73
M. m. koelzi												
Harvey Lake, Isle Royale	7	19	19	3	..	..	..	..	48	60.2	45 (94%)	3 (6%)
M. m. nachtriebi												
Forbes Lake, Isle Royale	1	2	1	5	1	..	..	..	10	62.5	4 (40%)	6 (60%)
Hatchet Lake, Isle Royale	..	..	..	1	3	..	..	..	4	65.1	..	4 (100%)
Lake Desor, Isle Royale	..	..	1	1	2	1	..	..	5	64.6	1 (20%)	4 (80%)
Porcupine Mts., Michigan	..	..	2	4	..	1	..	..	7	63.5	2 (29%)	5 (71%)
Upper Peninsula, Michigan	..	..	1	1	1	..	3	..	6	66.6	1 (17%)	5 (83%)
Lower Peninsula, Michigan	..	..	1	4	6	4	1	1	17	66.1	1 (6%)	16 (94%)
Glacier National Park, Montana	..	..	2	7	1	..	..	..	10	63.2	2 (20%)	8 (80%)
Sand Hills region, Nebraska	..	..	4	3	2	1	..	..	10	63.3	4 (40%)	6 (60%)
Missouri R. basin, North Dakota	..	..	2	3	2	1	..	..	8	63.9	2 (25%)	6 (75%)
Souris R., North Dakota	..	..	..	..	..	1	..	..	1	68.4	..	1 (100%)
Mississippi R. basin, Minnesota	..	..	1	2	..	..	..	..	3	63.3	1 (33%)	2 (67%)
Near Lake Nipigon, Ontario	..	2	6	3	..	..	..	..	11	61.2	8 (73%)	3 (27%)
Hudson Bay drainage, Ontario	..	..	2	7	11	11	3	2	36	66.2	2 (6%)	34 (94%)
Grand Lake, Quebec	..	..	..	..	1	..	1	1	3	68.7	..	3 (100%)
Miramichi, New Brunswick	..	..	..	..	1	1	..	..	2	66.1	..	2 (100%)
Penobscot R. basin, Maine	..	..	..	2	1	..	..	..	3	64.0	..	3 (100%)
Summary												
M. m. koelzi	7	19	19	3	..	..	..	..	48	60.2	45 (94%)	3 (6%)
M. m. nachtriebi	1	4	23	43	32	21	8	4	136	64.7	28 (21%)	108 (79%)

tributary to Lake Nipigon, between Orient Bay and Macdiarmid, Ontario. But these minnows are abnormally dwarfed and have a very long head with massive muzzle. Their relatively slenderer heads are attributable to an unfavorable environment. The next closest approach to *koelzi* is exhibited by specimens from Sand Hills, Nebraska, and these, too, are considerably dwarfed and, as a result, long-headed. The Sand Hills specimens approach *koelzi* also in the thinness of the lips, but in this respect the series from near Lake Nipigon is typical of *nachtriebi* (Table VII).

We name this subspecies for Dr. Walter Koelz, as a partial recognition of his contribution to the ichthyology of Isle Royale.

Couesius plumbeus plumbeus (Agassiz)

Lake northern chub

This minnow was reported by Ruthven (1906 : 109) for Washington Harbor, where Stanley also found it. Koelz took it only in Lake Desor. Ellsworth collected it in McCargoe Cove. In our 1945 collecting it proved to be one of the commonest fishes in the lower reaches of streams and about the entire shore of the island. Specimens were seined at stations L45 : 798, 800, 802, 803, 805, 806, 808 to 811, 814, 820, 821, 826, 830, 840, 845, 847, 849, and 851 (pp. 76–81). Seven-inch adults were taken in our experimental gill-nets, set in twenty to thirty-five feet of water in Middle Islands Passage (L45 : 847). That this chub has presumably inhabited Isle Royale for a long time is indicated by its isolated occurrence in Lake Desor, at an elevation of 235 feet above Lake Superior. That it was an early postglacial reinvader is suggested not only by its wide distribution in Canada (Dymond, 1947 : 19), but also by its place in the fauna of completely isolated lakes in the Huron Mountains on the south side of Lake Superior (Hubbs, 1929).

One hybrid between this species and the longnose dace, *Couesius p. plumbeus* × *Rhinichthys c. cataractae*, was identified in a series of lake northern chubs from the sluggish brown stream entering the extreme western end of Pickett Bay of Todd Harbor (L45 : 809).

Rhinichthys cataractae cataractae (Valenciennes)

Great Lakes longnose dace

In harmony with its far-northern limits (Dymond, 1947 : 20), this dace occurs commonly all around the island in effluent streams and stream mouths, and in Siskiwit Lake about the shore and in one tribu-

TABLE VII

Width of Lips in Northern Subspecies of Margariscus margarita

The over-all width across the lips near the middle is expressed as thousandths of the head length.

Subspecies and locality	N	R	M	42–57	58–87
M. m. koelzi					
Harvey Lake, Isle Royale	47	42–75	57.5	31 (66%)	16 (34%)
M. m. nachtriebi					
Forbes Lake, Isle Royale	10	56–71	64.9	3 (30%)	7 (70%)
Hatchet Lake, Isle Royale	4	66–73	70.0	. .	4 (100%)
Lake Desor, Isle Royale	5	67–83	75.8	. .	5 (100%)
Porcupine Mts., Michigan	7	43–77	64.1	2 (29%)	5 (71%)
Upper Peninsula, Michigan	6	63–83	71.3	. .	6 (100%)
Lower Peninsula, Michigan	17	56–81	67.6	1 (6%)	16 (94%)
Glacier National Park, Montana	10	57–71	62.7	1 (10%)	9 (90%)
Sand Hills region, Nebraska	10	54–66	60.2	4 (40%)	6 (60%)
Missouri R. basin, North Dakota	8	56–70	62.9	1 (13%)	7 (87%)
Souris R., North Dakota	1	62	61.7	. .	1 (100%)
Mississippi R. basin, Minnesota	3	60–67	64.3	. .	3 (100%)
Near Lake Nipigon, Ontario	11	46–76	64.1	2 (18%)	9 (82%)
Hudson Bay drainage, Ontario	36	54–87	71.7	1 (3%)	35 (97%)
Grand Lake, Quebec	3	73–82	77.3	. .	3 (100%)
Miramichi, New Brunswick	2	65–78	71.5	. .	2 (100%)
Penobscot R. basin, Maine	3	56–61	59.7	1 (33%)	2 (67%)
Summary					
M. m. koelzi	47	42–75	57.5	31 (66%)	16 (34%)
M. m. nachtriebi	136	43–87	67.4	16 (12%)	120 (88%)

tary. Stanley seined some young specimens at the mouth of the Little Siskiwit River, but in 1945 we failed to get it either there or upstream to one-half mile above the mouth. The 1945 collecting stations were L45 : 800, 802, 803, 806, 808, 810, 811, 819 to 821, 826, 830, 838, 839, 841, 848, and 849 (pp. 76–81). An adult male specimen taken on July 19 (L45: 806) was still in breeding color.

Pfrille neogaea (Cope)

Finescale dace

This northern species is quite rare on Isle Royale. It was recorded from Sumner Lake by Ruthven (1909 : 300) and was obtained in the same lake and in an adjacent marsh pool by Koelz, who also collected it in Benson and Wallace lakes. In 1945 we took it in sluggish water in the outlet of Hatchet Lake (L45 : 807); in the small bog pond about 100 feet inshore, approximately 1.25 miles east of Long Point (L45 : 824); in the lower, slow-moving part of the outlet of Lake Halloran (L45 : 826); and abundantly in high-lying Lily Lake (L45 : 817). Its occurrence at this high elevation (about 400 feet above Lake Superior) suggests that it first arrived long ago on Isle Royale. This suggestion is in harmony with the fact that the species is very widely spread in Canada (Dymond, 1947 : 20).

Chrosomus eos Cope

Northern redbelly dace

The northern redbelly dace is also rare on Isle Royale. Koelz took it only in Wallace Lake. In our collections it was found in the boggy stream entering the west end of Pickett Bay of Todd Cove (L45 : 809); near the Lake Superior shore in the small bog pond about 1.25 miles east of Long Point (L45 : 824); and in the lower reaches of the outlet of Wallace Lake (L45 : 849). On the island, as elsewhere, its distribution is obviously related to that of the finescale dace (*Pfrille*). They occurred together in two of our 1945 collections (L45 : 809 and 824). At station L45 : 824 a hybrid, *Chrosomus eos* × *Pfrille neogaea,* was taken (these species often hybridize). *Chrosomus eos* ranges throughout Ontario to 52° N. Lat. (Dymond, 1947 : 20).

Notemigonus crysoleucas auratus (Rafinesque)

Western golden shiner

This sluggish-water fish was taken by Koelz in ten of the inland lakes (Table IV). It occurred in six of our 1945 collections: L45 : 798, 802, 803, 814, 840, and 843 (pp. 76–79). Four of these stations were in lake outlets (including those of three lakes in which Koelz found the fish), and two were in and about the mouths of streams entering sheltered coves of Lake Superior. On Isle Royale *Notemigonus* occurs only in the lower waters and finds there its approximate northern limit, east of the plains. It is known in Ontario north to Lake Abitibi, but has not been reported from Lake Nipigon (Dymond, 1947 : 20). For these reasons it is regarded as one of the latest reinvaders of northern glaciated areas.

Notropis atherinoides : *acutus* Lapham × *atherinoides* Rafinesque
Emerald shiner intergrades

Isle Royale specimens of this shiner are interpreted as intergrades between the lake emerald shiner and the river emerald shiner. The intergrades are intermediate in the diagnostic characters (Table VIII). In three of the six characters they incline toward *atherinoides;* in two they are almost exactly intermediate; and in one they approach *acutus.*

TABLE VIII

COMPARISON OF ISLE ROYALE INTERGRADES WITH NOTROPIS ATHERINOIDES ACUTUS (FROM LAKE MICHIGAN) AND N. A. ATHERINOIDES (FROM LAKE ERIE)

The comparisons are based on well-preserved adults. The measurements were made according to the methods proposed by Hubbs and Lagler (1941, 1947). The data for the two subspecies are taken from Hubbs, 1945 : 15. The nine Isle Royale specimens measured were 56 to 58 mm. in standard length. Eight were from collection L45 : 800 and one was from L45 : 820.

Character	*N. a. acutus*	Isle Royale intergrades Average (range)	*N. a. atherinoides*
$\frac{\text{Body depth}}{\text{Body width}}$	< 2.0	1.98 (1.9–2.1)	> 2.0
$\frac{\text{Head length}}{\text{Body width}}$	< 2.0	2.17 (2.0–2.5)	> 2.0
$\frac{\text{Length of depressed dorsal fin}}{\text{Body width}}$	Typically 1.4–1.5 Range 1.2-1.7	1.71 (1.6–2.0)	Typically 1.6–1.8 Range 1.4-2.0
$\frac{\text{Standard length}}{\text{Head length}}$	> 4.0	4.09 (3.9–4.3)	< 4.0
$\frac{\text{Distance from dorsal fin to occiput}}{\text{Length of depressed dorsal fin}}$	> 2.0	1.89 (1.7–2.1)	< 2.0
$\frac{\text{Head length}}{\text{Upper jawlength}}$	3.3–3.5	3.48 (3.3–3.6)	3.6–3.8

On Isle Royale proper this fish is known only from Siskiwit Lake, where it was collected by Koelz. In the marginal waters it proved much less common than was expected, since the species is abundant in some places around the mainland shores of Lake Superior. In our 1945 collecting it was found only in stream mouths (L45 : 800, 802, and 820).

Notropis hudsonius hudsonius (Clinton)
Northern spottail shiner

Koelz took the spottail shiner in ten inland lakes, including Siskiwit Lake (Table IV). In 1945 it was collected in the same lake and at five stations scattered around the island in the lower parts of streams and on the shore. The station numbers were L45 : 802, 803, 805, 838, 840, and 843 (pp. 76–79).

The spot at the base of the tail fin is extreme in this material, as it also is in specimens from Carp Lake in the Porcupine Mountains, on the south side of Lake Superior. It is about one third as wide as the caudal peduncle is at the same vertical, and it is intensely black and round. A single young specimen was found in sorting Koelz's collection from Harvey Lake, one of the higher bodies of water and the scene of subspeciation of the three other cyprinids present. It is thought almost certain that this fish was inadvertently mixed with this collection, but the circumstance is mentioned to induce future collectors to search for this minnow in Harvey Lake. Ruthven (1906 : 108) reported the species from Carp Lake. It ranges far northward in Canada (Dymond, 1947 : 21).

Notropis heterodon (Cope)
Blackchin shiner

The blackchin shiner is known on Isle Royale only from the outlet of Sargent Lake, near its mouth in McCargoe Cove (L45 : 803). The three specimens that were collected probably were strays from the lake, from which, however, the species has not been taken. They appear to be typical. Each has eight anal rays.

This species is a usual inhabitant of clear weedy lakes through the southern part of the glacial district and occurs elsewhere in the Lake Superior basin. Dymond (1947 : 21) recorded it as ranging northward in Ontario only to Sault Sainte Marie, but Smith and Moyle (1944 : 121) collected it in a Minnesota stream on the north shore of Lake Superior. It was probably one of the last postglacial immigrants.

Notropis volucellus volucellus (Cope)

Northern mimic shiner

Another fish of restricted occurrence on Isle Royale is the northern mimic shiner. Koelz took it only in Lake Richie, where he found it common. In 1945 we took it in the lower reaches of the westernmost tributary of Chippewa Harbor (L45 : 840), in the outlet of Lake Richie near its mouth (L45 : 841), and, downstream, in the Mason Lake outlet (L45 : 843). All these localities are in the drainage of Chippewa Harbor.

In Canada this minnow ranges at least to 52° N. Lat. (Dymond, 1947 : 21). It is the species that Dymond had listed earlier (1926 : 50) from Lake Nipigon as *Notropis deliciosus stramineus.*

Notropis heterolepis heterolepis Eigenmann and Eigenmann

Northern blacknose shiner

This shiner, which has a far northern range (Dymond, 1947 : 22), is the commonest cyprinid on the island. In 1929 Koelz took it in twenty-one inland lakes (Table IV); in 1930 Stanley collected a series in the mouth of Big Siskiwit River; and in 1945 Lagler secured it in one stream collection (L45 : 802 in part) and in five stream-mouth stations: L45 : 800, 802 in part, 803, 841, and 846 (pp. 76–79). The characters of the blacknose shiner from most of these localities are in general similar to those shown by the subspecies throughout its range. It is noteworthy, therefore, that Harvey Lake is inhabited by an apparently distinct subspecies. As is indicated below, however, the specimens from certain other lakes are intermediate in some respects.

Notropis heterolepis **regalis,** new subspecies

Harvey Lake blacknose shiner

(Pl. II, Fig. 3)

In its typical form this race of *Notropis heterolepis* appears to be confined to Harvey Lake, Isle Royale, which it occupies in company with two other endemic subspecies (*Margariscus margarita koelzi* and *Pimephales promelas harveyensis*).

Type specimens.—The holotype, 81 mm. in standard length, was collected by Walter Koelz on September 1, 1929. It is deposited in the University of Michigan Museum of Zoology (No. 100027), along with 108 paratypes 22 to 74 mm. long (U.M.M.Z., No. 100028). These specimens were seined on the shoals (Pl. I, Fig. 2) of Harvey Lake. The 23 additional paratypes, 32 to 48.5 mm. long (U.M.M.Z., No. 144474), were collected by Lagler at station L45 : 813, under somewhat different conditions, at the source of the outlet (Pl. I, Fig. 3).

Diagnosis.—Like *N. h. heterolepis,* but reaching a relatively huge size (81 mm. in standard length), and with the head small, usually entering the standard length more than 4.0 times, the eye also small, and the lateral band rather solidly black. The differences in head and eye proportions are apparent not only between specimens of maximum size, but also between those of the same size.

The large size attained in Harvey Lake probably has some genetic basis, for it is the maximum known for the species, and the lake has no apparent peculiar richness; the other species in the lake are not particularly large or robust. Among 697 series of *N. h. heterolepis* catalogued in the University of Michigan Museum of Zoology, ranging from North Dakota to Maine and Nova Scotia and comprising 27,874 specimens, the maximum size very seldom reaches 60 mm., exceeds 62 mm. in only five lots, and exceeds 70 mm., reaching 71 mm., in only one series (U.M.M.Z., No. 108077), that from Muskellunge Lake, Vilas County, Wisconsin.

In the small size of the head and the eye (Tables IX–X) the Harvey Lake blacknose shiner contrasts sharply with typical *N. h. heterolepis* throughout its wide east–west expanse of range. After handling nearly all the material mentioned above, we recognized the difference. When the proportions at the different size groupings for Harvey Lake are compared with those for a series from Lake Odessa, Frontenac County, Ontario (selected because of the many well-preserved specimens of typical appearance), there is seen to be very little overlap. We believe that similar results would be obtained if the Harvey Lake fish were compared with those from most other localities. Several lots from Isle Royale have the head and eye as long as is usual in *N. h. heterolepis,* but those from some other lakes are intermediate for one or both characters in one or more size groups. In no other lot, however, is the average as low for either head or eye proportion as it is in the Harvey Lake fish. Furthermore, the approach toward *regalis* is almost confined to the smallest size group. The specimens from Muskellunge Lake, Wisconsin, where the species reaches the largest size known except in Harvey Lake, have the

TABLE IX

Comparison by Lakes of Head Lengths of Notropis heterolepis

In the body of the table the figures in the first line for each rubric are the observed range and, in parentheses, the mean; those in the second line are the number of specimens and, in parentheses, the percentage separable above (+) or below (—) the arbitrary line of separation indicated in column heading. The head length, including opercular membrane, is expressed in thousandths of the standard length.

Size group, mm. Line of separation	27–40 271–272	40–50 263–264	50–60 256–257	60–81 256–257
N. h. regalis				
Harvey L., Isle Royale	244–273 (259) 49 (98 —)	246–261 (251) 7 (100 —)	238–257 (246) 15 (93 —)	239–260 (246) 32 (94 —)
N. h. heterolepis				
L. Odessa, Ontario	270–287 (280) 26 (92 +)	265–289 (278) 14 (100 +)	256–283 (273) 46 (98 +)	. . . . . .
Muskellunge L., Wisconsin	267–277 (271) 9 (56 —)	272–273 (273) 2 (100 +)	252 1 (100 —)	256–281 (267) 14 (93 +)
N. h. heterolepis and intermediates				
Isle Royale lakes				
Beaver L.	269–283 (277) 22 (95 +)	266–301 (277) 26 (100 +)	. . . . . .	. . . . . .
L. Benson	256–274 (264) 10 (90 —)	. . . . . .	. . . . . .	. . . . . .
Chickenbone L. outlet	269–285 (275) 10 (70 +)	272–288 (277) 10 (100 +)	. . . . . .	. . . . . .
L. Eva	272 1 (100 +)	260 1 (100 —)	. . . . . .	. . . . . .
Forbes L.	269–278 (272) 5 (60 —)	271 1 (100 +)	. . . . . .	. . . . . .
Intermediate L.	264–279 (271) 10 (50 ±)	265–282 (272) 10 (100 +)	. . . . . .	. . . . . .
L. John	266–283 (274) 10 (60 +)	. . . . . .	. . . . . .	. . . . . .
Linklater L.	262–268 (266) 2 (100 —)	. . . . . .	. . . . . .	. . . . . .
L. Livermore	263–272 (267) 5 (80 —)	263–272 (268) 5 (80 +)	. . . . . .	. . . . . .
L. Mason	296–296 (296) 2 (100 +)	283 1 (100 +)	. . . . . .	. . . . . .
Mud L.	262–270 (267) 5 (100 —)	. . . . . .	. . . . . .	. . . . . .
Otter L.	264–277 (270) 5 (60 —)	257–281 (271) 5 (80 +)	. . . . . .	. . . . . .
L. Richie	276–290 (281) 11 (100 +)	268–293 (277) 12 (100 +)	. . . . . .	. . . . . .
Sargent L. and outlet	268–285 (276) 7 (57 +)	270–277 (274) 5 (100 +)	. . . . . .	. . . . . .
Sholts L.	267–280 (274) 6 (50 ±)	. . . . . .	. . . . . .	. . . .
Siskiwit L.	270–289 (278) 17 (88 +)	273–281 (277) 5 (100 +)	. . . . . .	. . . . .
Sumner L.	267–268 (267) 2 (100 —)	262–274 (267) 5 (60 +)	272–281 (277) 2 (100 +)	. . . . . .
L. Theresa	268–287 (278) 6 (60 +)	267–288 (277) 6 (100 +)	. . . . . .	. . . . . .
Wallace L.	268–280 (274) 2 (50 ±)	. . . . . .	. . . . . .	. . . . . .

head on the average almost as large as those in Lake Odessa, though the eye measurements are atypically low—owing to the unusual width of the soft margin of the orbit anteriorly.

TABLE X

COMPARISONS BY LAKES OF ORBIT LENGTHS OF NOTROPIS HETEROLEPIS

The format is explained in the subheading of Table IX. The orbit was measured between free rims, from just behind nostril to lower edge of dark lateral stripe.

Size group, mm. Line of separation	27–40 77–78	40–50 72–73	50–60 68–69	60–81 66–67
N. h. regalis				
Harvey L., Isle Royale	67–81 (74) 49 (80 –)	67–70 (68) 7 (100 –)	60–69 (65) 15 (87 –)	57–68 (63) 32 (94 –)
N. h. heterolepis				
L. Odessa, Ontario	73–91 (81) 26 (81 +)	74–83 (77) 14 (100 +)	68–79 (73) 46 (98 +)	... ...
Muskellunge L., Wisconsin	72–78 (75) 9 (78 –)	68–72 (70) 2 (100 –)	68 1 (100 –)	62–74 (68) 14 (57 +)
N. h. heterolepis and intermediates				
Isle Royale lakes				
Beaver L.	76–89 (83) 22 (95 +)	74–87 (80) 26 (100 +)	... ...	... ...
L. Benson	72–80 (76) 10 (80 –)	... ...	... ...	... ...
Chickenbone L. outlet	76–88 (82) 10 (90 +)	76–87 (81) 10 (100 +)	... ...	... ...
L. Eva	85 1 (100 +)	76 1 (100 +)	... ...	... ...
Forbes L.	76–83 (79) 5 (60 +)	76 1 (100 +)	... ...	... ...
Intermediate L.	72–87 (79) 10 (60 +)	74–82 (78) 10 (100 +)	... ...	... ...
L. John	72–78 (75) 10 (70 –)	... ...	... ...	... ...
Linklater L.	89–89 (89) 2 (100 +)	... ...	... ...	... ...
L. Livermore	74–82 (79) 5 (80 +)	74–78 (76) 5 (100 +)	... ...	... ...
L. Mason	77–79 (78) 2 (50 ±)	75 1 (100 +)	... ...	... ...
Mud L.	74–82 (80) 5 (80 +)	... ...	... ...	... ...
Otter L.	74–82 (79) 5 (60 +)	76–82 (79) 5 (100 +)	... ...	... ...
L. Richie	79–88 (83) 11 (100 +)	79–88 (83) 12 (100 +)	... ...	... ...
Sargent L. and outlet	78–90 (84) 7 (100 +)	77–84 (80) 5 (100 +)	... ...	... ...
Sholts L.	75–81 (79) 6 (83 +)	... ...	... ...	... ...
Siskiwit L.	79–90 (83) 17 (100 +)	79–85 (82) 5 (100 +)	... ...	... ...
Sumner L.	77–78 (77) 2 (50 ±)	70–82 (77) 5 (80 +)	73–74 (73) 2 (100 +)	... ...
L. Theresa	79–85 (82) 6 (100 +)	71–79 (75) 6 (83 +)	... ...	... ...
Wallace L.	85–88 (87) 2 (100 +)	... ...	... ...	... ...

We conclude that *N. h. regalis,* though rather sharply distinct from *N. h. heterolepis,* is approached by the races inhabiting certain other inland lakes, particularly those on Isle Royale. Were it not for such partial transition, full specific status might have been considered.

We apply the name *regalis* to this species in reference both to its large size and to its occurrence on Isle Royale.

Pimephales promelas promelas Rafinesque
Northern fathead minnow

In view of its northern range (Dymond, 1947 : 22), it is not surprising that this minnow has been taken on Isle Royale. The first island record, by Ruthven (1909 : 330), was for Sumner Lake. Koelz found it extremely abundant in this lake in 1929 and took it also in Hatchet and Wallace lakes. In 1945 it was obtained near Lake Superior in the outlet of Sumner Lake (L45 : 846). Large numbers were found in Lily Lake (L45 : 817), the highest body of water on the island. This isolated lake, which was not worked by Koelz, lies above the 1,000-foot contour in the western part of the island. At the suggestion of Karl Gilbert, it is designated "Lily Lake." Six northern fathead minnows from this small body of water have 46–50 scale rows, which is the normal number for the typical subspecies in this latitude. In all the island waters except Harvey Lake the characters of the fathead minnows agree well with those of *P. p. promelas* elsewhere in the far north. The Harvey Lake population is taken to represent an endemic subspecies.

Pimephales promelas **harveyensis,** new subspecies
Harvey Lake fathead minnow

(Pl. II, Fig. 4)

As Koelz pointed out to Hubbs, the fathead minnows of Harvey Lake are quite unlike those from other waters throughout the wide range of the species. They seem worthy of subspecific separation, as do the representatives in the same lake of *Margariscus margarita* and *Notropis heterolepis.*

Type specimens.—The holotype, 51 mm. in standard length, was collected by Walter Koelz in Harvey Lake on Isle Royale on September 1, 1929. It is deposited in the University of Michigan Museum of Zoology (No. 99989). Seventy-nine paratypes (U.M.M.Z., No. 99990), 22 to 48 mm. long, were collected at the same time and place. About the head of the outlet, on July 11, 1945, Lagler collected 24 additional paratypes (U.M.M.Z., No. 144475): 15 young, 14 to 17 mm. long, and 9 half-grown to adult specimens, 36.5 to 47 mm. long.

Diagnosis.—Like *P. p. promelas,* but with finer scales (in 50–60 rows); dorsal fin inserted farther forward; caudal peduncle longer and slenderer; head short, slender, and subconic; eye small; mandible not very strongly oblique. The lateral line is short, as in *P. p. promelas* as contrasted with *P. p. confertus.*

On the basis of the scale count 90 per cent of the specimens of *P. p. harveyensis* from Harvey Lake can be separated from 94 to 100 per cent of the specimens of *P. p. promelas* from the other localities inhabited by the species on Isle Royale (Table XI).

TABLE XI

Scale Counts Along Side of Body of Pimephales promelas from Isle Royale

Subspecies and locality	N	R	M	45–51	52–60
P. p. harveyensis					
Harvey Lake	78	50–60	54.0	8 (10%)	70 (90%)
P. p. promelas					
Hatchet Lake	10	45–50	47.6	10 (100%)	..
Sumner Lake	10	46–51	48.3	10 (100%)	..
Wallace Lake	17	45–53	48.8	16 (94%)	1 (6%)
Lily Lake	6	46–50	..	6 (100%)	..

The origin of the dorsal fin is unusually far forward. Its distance from the caudal base reaches, when measured forward, to any point from the anteriormost part of the eye to a location nearer to the tip of the snout than to the nostril. In Sumner Lake and Lily Lake specimens this measurement reaches to any point from well behind the eye to the anterior part of the eye. In this respect, as well as in other proportions, the Hatchet Lake specimens are somewhat intermediate.

The difference in proportions are already evident in the very young (14 to 17 mm. long) — a strong indication of genetic fixation. Furthermore, the melanophores of the back are fewer and larger than those in comparable young of *P. p. promelas* from Isle Royale, and the dark back is more restricted and is more sharply set off by a light streak from the dark lateral band.

Except for the darker color, the specimens collected by Lagler about the source of the outlet (Pl. I, Fig. 3) are essentially like those taken along the main lake shore (Pl. I, Fig. 2).

Although detailed comparison is not made with collections of *P. p.*

promelas from various parts of the range of the typical subspecies, our experience with the group indicates that the characters of the Harvey Lake specimens are extreme and warrant the erection of this subspecies. The contrast is particularly sharp with the coarse-scaled, heavy-set race that occupies the southern part of the Great Lakes basin. As indicated by Hubbs and Black (1947:8), *P. p. promelas* will probably be broken up after detailed analysis, into two or more subspecies.

ESOCIDAE — PIKE FAMILY

Esox lucius Linnaeus

Northern pike

Pike are widely distributed in the inland lakes and around the shores of Isle Royale. Ruthven (1909 : 330) indicated Sargent Lake as the only Isle Royale record then known for this fish, but in 1929 Koelz found it not only there but also in twenty-seven other inland lakes (Table IV). On the authority of Karl Gilbert, Lake Benson may now be added to the list. In 1945 pike were collected in the lower parts of the outlets of Sargent Lake (L45 : 803) and in Lakes Richie (L45 : 841) and Mason (L45 : 842). According to reports of anglers and others, it occurs in most of the coves around the island, one of which is named Pickerel Cove. The 1945 shore records include: Todd Harbor (L45 : 812); Washington Harbor (report, Gilbert); and Duncan Bay (report, Allen). Catches of "grass pike," occasionally entered on the commercial fish tallies for Lake Superior around the island, are referable to this species.

Esox masquinongy masquinongy Mitchill

Great Lakes muskellunge

The muskellunge is included in the list of Isle Royale fishes solely on the basis of Ruthven's record (1906 : 109) of one caught in Washington Harbor. The specimen was probably not preserved, for it is not recorded in the University of Michigan Museum of Zoology. A confirmation of the report would therefore be welcome.

GADIDAE — COD FAMILY

Lota lota maculosa (LeSueur)

American burbot

Ruthven (1909 : 331) reported the burbot, locally called "lawyer," from Tobin and Rock harbors, and Dr. Van Oosten saw some that had been caught in Chippewa Harbor. Lagler took specimens in experimental gill-nets at a depth of fifty feet in Lane Cove (L45 : 797) and at 20–35 feet in Middle Islands Passage (L45 : 847). Gilbert reported specimens taken by commercial fishermen in Washington Harbor. From these records and reports it is concluded that the fresh-water representative of the cod family is distributed all around the island. In the inland waters it must be of very restricted occurrence, since in his extensive gill-net collecting Koelz took it in Siskiwit Lake only.

The American representative of the Holarctic species *Lota lota* has a far northern range (Hubbs and Schultz, 1941:17–27).

PERCOPSIDAE — TROUTPERCH FAMILY

Percopsis omiscomaycus (Walbaum)

Troutperch

At Isle Royale the troutperch occurs in all marginal waters as well as in the interior. The first report, by Ruthven (1909 : 331), under the name *P. guttatus,* was for Tobin Harbor. Koelz collected it in six inland lakes (Table IV), and Stanley seined one young specimen at the mouth of the Little Siskiwit River. In 1945 the species was commonly encountered in the lower reaches of streams tributary to Lake Superior as well as along the shore. It was taken at stations L45 : 798, 802, 803, 805, 811, 820, 830, 839, 843, 849, and 850 (pp. 76–81). In line with experience elsewhere around the Great Lakes, in shore collections it was seined most commonly after dark. A ripe female obtained on July 18 at station L45 : 805 gave evidence of delayed spawning, attributable to the persistently low temperatures of Lake Superior waters. The species is one of far northern limits (Dymond, 1947 : 25).

PERCIDAE — PERCH FAMILY

Perca flavescens (Mitchill)

Yellow perch

On Isle Royale the perch is principally a fish of the inland lakes, in most of which it occurs (in twenty-eight out of thirty-nine). It also lives, scatteringly, about the lake shore and in stream mouths. It was reported from Washington Harbor by Ruthven (1906 : 109), by commercial fishermen, and by Gilbert in 1945; from Forbes Lake by Ruthven (1909 : 331) and by Koelz; and from Harvey Lake by Koelz and by Lagler (L45 : 813). The other 1945 collections were L45 : 802, 803, 811, 840, 841, 843, and 845 (pp. 76–79). See also Table IV.

The perch ranges far to the north in Canada, as does the following species (Dymond, 1947 : 27).

Stizostedion vitreum vitreum (Mitchill)

Yellow pikeperch

This fish, sometimes locally called "walleye" or "yellow pickerel," was taken by Koelz from three lakes only (Chickenbone, Whittlesey, and Dustin). Examples from these inland lakes are very peculiar in appearance. When studied more closely they may prove to represent distinct local forms. The only commercial listing seen is of a catch made in Chippewa Harbor. Karl Gilbert reports that it is occasionally taken in Washington Harbor. The species no doubt occurs in other places about the shore of Isle Royale, since it is found elsewhere in Lake Superior and tributary waters.

Percina caprodes semifasciata (De Kay)

Northern logperch

Although it also has far northern limits (Dymond, 1947 : 27), the logperch is restricted in its known distribution to the central part of the island near the southern shore. It was collected by Koelz only in Siskiwit, Whittlesey, and Dustin lakes, all of which lie between the Nipissing and the Minong water planes. Lagler also found this darter in Siskiwit Lake (L45 : 836 and 838), as well as in the lake outlet below the falls (L45 : 839). The circumstance that *Percina* retains an air bladder during its juvenile midwater stage helps to explain how it may have crossed the deep channel that separates Isle Royale from the mainland. Though it ranges far north in Canada, its absence from the higher waters of Isle Royale, the Huron Mountains, and the Porcupine Mountains suggests that it was not among the earlier postglacial immigrants.

Poecilichthys exilis (Girard)

Iowa darter

The taking of this darter only in Chickenbone and Sargent lakes (by Koelz) is one of the many interesting results of the ichthyological investigation of the island. Its occurrence at this latitude is not unexpected, for Dymond (1947 : 28) reported it from much farther north. The surprising circumstances are: first, that a minute bottom-swimming fish without an air bladder and showing a decided preference for weedy situations should ever have swum across the deep channel to the island;

and, second, that, so far as known, after arriving on the island it should have survived only in two lakes, with outlets in close proximity.

CENTRARCHIDAE — SUNFISH FAMILY

Lepomis gibbosus (Linnaeus)

Pumpkinseed

The occurrence of this sunfish on Isle Royale was hardly to be expected, but Koelz took it in Lakes Richie and Mason, and Lagler found it in the outlet of Sargent Lake (L45 : 803). There is no reason to suspect that it was introduced. On Isle Royale it may represent a relict from a warm postglacial period, for it is not now known from waters on the adjacent mainland (Radforth, 1944 : 65–67; Dymond, 1947 : 29; Eddy and Surber, 1947 : 238), unless a record from Baptism River, eastern Minnesota (Smith and Moyle, 1944:123), represents a native population. Specimens reputedly from the Red River of the North, labeled as collected in the Saskatchewan River by S. H. Scudder (Museum of Comparative Zoölogy, No. 3502, seven specimens, received April 28, 1860, one now in the University of Michigan Museum of Zoology) suggests the occurrence of the species much farther north than has commonly been indicated. We understand that recent findings by Canadian ichthyologists confirm this suggestion.

COTTIDAE — SCULPIN FAMILY

Triglopsis thompsonii Girard

Deepwater sculpin

From Isle Royale this sculpin is known only on the basis of specimens found by Ruthven (1909 : 331) in the stomachs of lake trout caught off the "east coast." It is no doubt common, however, in deep water all around the island. It inhabits all the Great Lakes, including Lake Nipigon, and the same form, or a similar derivative of the Arctic marine *Triglopsis quadricornis*, occurs in rivers that flow into the Arctic Ocean (Hubbs, 1926:73–74; Hubbs and Lagler, 1947:97).

Cottus ricei Nelson

Spoonhead muddler

Koelz took this interesting species in three of the inland lakes of Isle Royale, namely, Siskiwit, Whittlesey, and Desor. Lagler found it in Siskiwit Lake outlet (L45 : 839) and in other stream stations as well as on the shore: L45 : 808, 811, 822, and 830 (pp. 77–79). It may be assumed to occur scatteringly about the entire island, since it is principally a fish of the shore habitat and is of wide range in Canada (Dymond, 1947 : 30). Its occurrence in three lakes and in streams on Isle Royale is an example of the tendency of fishes of the Great Lakes proper to enter smaller waters in the north. In other parts of Michigan *C. ricei* inhabits very few of the inland lakes. The records on Isle Royale confirm the view that it was one of the earliest of the postglacial immigrants. All specimens collected in 1945 were more or less covered with the dermal prickles that usually characterize this muddler.

Cottus bairdii kumlieni (Hoy)
Great Lakes muddler

As "*Cottus ictalops*" this muddler was recorded by Ruthven (1906 : 109; 1909 : 331) from Washington and Rock harbors. Koelz took it in Chickenbone Lake, one of the very few inland lakes known to be inhabited by this subspecies. In 1945 we collected it in stream mouths (including that of the Little Siskiwit River, where Stanley also found it) and at various shore stations more or less around the entire island. These collections were L45 : 798, 799, 805, 811, 830, 835, 843, 848, 850, and 852 (pp. 76–81).

Although the differences between the Great Lakes muddler and the common slimy muddler (*C. cognatus gracilis*) are reasonably trenchant, the characters are subject to much variation and, individually, to some overlap, and certain characters are not useful in small specimens. We have therefore prepared a summary, based on Isle Royale material, of the contrasting characters of the two species (Table XII).

Cottus cognatus gracilis Häckel
Common slimy muddler

Under the name *Uranidea franklini,* then current, Ruthven (1909: 331) reported this cold-water member of the sculpin family from Rock Harbor and from Benson Brook. Koelz took it in six inland lakes (Table IV). During our 1945 collecting in streams we found it more often than the Great Lakes muddler and also obtained it in stream mouths and at shore stations. It is, therefore, distributed all around the island. The station numbers are L45 : 803, 810, 811, 814, 819, 820, 830, 839 to 841, 843, and 852 (pp. 76–81). In Table XII are given distinctions between this species and the Great Lakes muddler (*C. bairdii kumlieni*).

TABLE XII

COMPARISON OF ISLE ROYALE SPECIMENS OF COTTUS BAIRDII KUMLIENI AND COTTUS COGNATUS GRACILIS COLLECTED IN 1945

Frequency of anal ray counts

	9	10	11	12	13	14	Mean
C. b. kumlieni	. .	. .	. .	6	25	8	13.1
C. c. gracilis	3	18	22	5	. .	. .	10.4

Frequency of pelvic soft-ray counts

	Formula (left–right)				Each fin	
	3–3	3–4	4–3	4–4	3	4
C. b. kumlieni	2	. .	4	33	8	70
C. c. gracilis	45	. .	3*	. .	93	3*

Frequency of sums of number of rays in anal and in both pelvic fins

	15	16	17	18	19	20	21	22	Mean
C. b. kumlieni	. .	. .	. .	. .	2	9	19	9	20.9
C. c. gracilis	3	19	22	2	2	. .	. .	. .	16.6

Nonmeristic characters

Character	*C. b. kumlieni*	*C. c. gracilis*
Index of anus position in larger specimens†	Usually more than 0.5	Usually less than 0.5
Palatine teeth in larger specimens	Usually present (present on one or both sides in 15 out of 20 examined)	Usually lacking (absent in all six larger specimens)
Spots on anal fin	Darker	Fainter or lacking
Under side of chin.	Conspicuously mottled (entirely dark in breeding males)	Not definitely mottled, nearly uniform, light or evenly dusky

* The innermost, fourth, ray was rudimentary in these three specimens.

† The index of anus position is the fraction in tenths of the caudal fin that is covered when the distance from the tip of the snout to the anus is stepped backward from the anus onto the caudal fin. In the smaller specimens the index is lower in each form, but the distinction between the species holds fairly well.

GASTEROSTEIDAE — STICKLEBACK FAMILY

Eucalia inconstans (Kirtland)

Brook stickleback

The northerly range of this species (Dymond, 1947 : 31) is in harmony with its occurrence on Isle Royale, though its usual bog-water habitat seems incongruous with the concept that it crossed the deep channel. Ruthven (1909 : 331) recorded it from tamarack and spruce swamps about Siskiwit Lake; Koelz found it in six other inland lakes (Table IV); and Lagler collected it in two additional ones. Our 1945 collecting showed this species to be one of the more common kinds on the island, occurring in ponds, including those formed by beaver dams, in streams, in stream mouths, and, as strays in one collection, along the Lake Superior shore. Boggy habitats appear to be preferred. The 1945 collecting stations were L45 : 798, 799, 807, 809, 810, 813, 815, 817, 820, 821, 823, 824, 826 to 828, 846, 850, 851, and 852 (pp. 76–81). Several specimens taken during the latter half of July and early August were in breeding condition. The females were ripe, and the males showed the characteristic black breeding color.

Pungitius pungitius (Linnaeus)

Ninespine stickleback

In addition to the many localities, principally stream mouth and shore, in which we collected this Arctic and Subarctic stickleback, several other records attest a general though chiefly marginal distribution about the island. Our stations are L45 : 799, 805, 811, 814, 815, 821, 835, 843, 846, 848, 849, and 851 (pp. 76–81). Previous records are those of Ruthven (1909 : 331) for Rock and Tobin harbors; of Koelz for three inland lakes (Siskiwit, Hatchet, and Desor); of Ellsworth for the mouth of Washington River; and of Stanley for the mouth of Little Siskiwit River. Throughout Michigan it is essentially confined to the shores of the Great Lakes and occurs in very few of the inland lakes. Its somewhat wider distribution on Isle Royale is in harmony with the northern latitude of the island, for in the far north this species, like several other fishes, occurs commonly in the smaller waters.

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PLATES I–II

FIG. 1. Harvey Lake and surroundings, Isle Royale

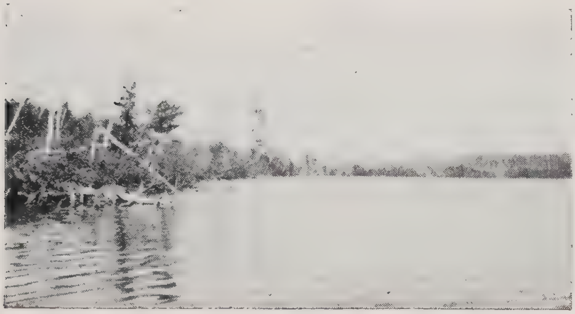

FIG. 2. Harvey Lake, north shoreline, looking east from outlet

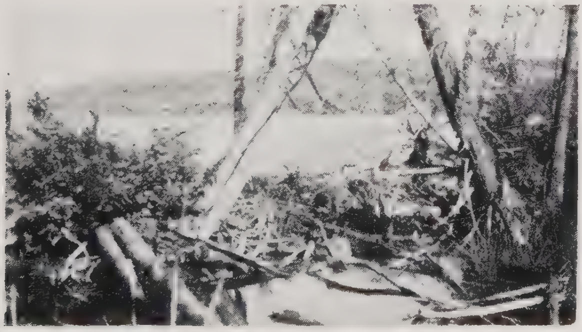

FIG. 3. Beaver dam, Harvey Lake outlet (most of Fig. 1 may be seen in background)

(All photographs by Karl F. Lagler, July, 1945)

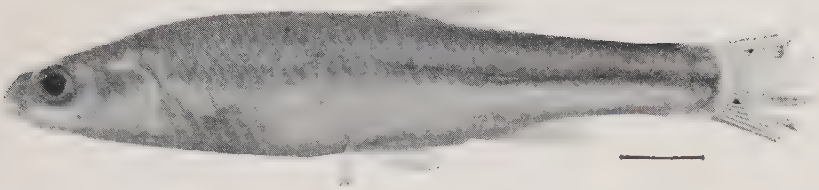

FIG. 1. *Margariscus margarita koelzi:* the holotype, 84 mm. in standard length, from Harvey Lake, Isle Royale, Michigan

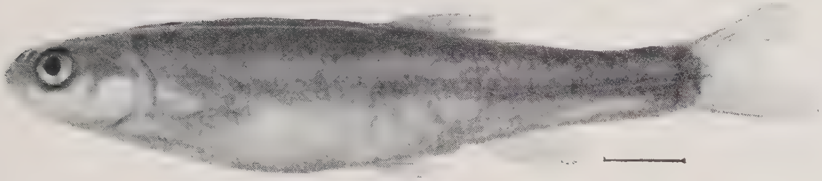

FIG. 2. *Margariscus margarita nachtriebi:* an adult, 80.5 mm. long, collected in Lake Desor, Isle Royale, by Walter Koelz, September 10, 1929

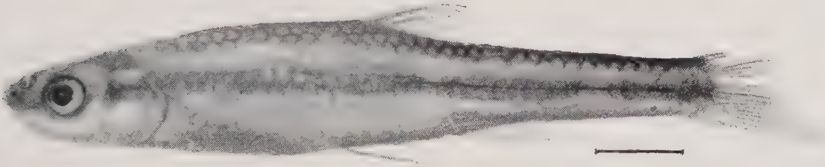

FIG. 3. *Notropis heterolepis regalis:* the holotype, 81 mm. long, from Harvey Lake, Isle Royale, Michigan

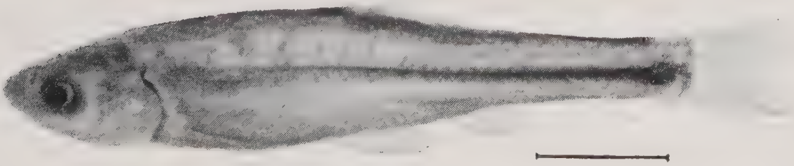

FIG. 4. *Pimephales promelas harveyensis:* the holotype, 51 mm. long, from Harvey Lake, Isle Royale, Michigan

(The scale bar equals one centimeter.)

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THE POSTEMBRYONIC DEVELOPMENT OF THE COPEPOD *PSEUDODIAPTOMUS EURYHALINUS* JOHNSON, AND ITS PHYLOGENETIC SIGNIFICANCE[1]

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INTRODUCTION

The genus *Pseudodiaptomus* is of special interest to marine and fresh-water biologist alike. This arises especially because of the unique systematic and biologic position occupied by the species. Its close relationship to the fresh-water genus *Diaptomus* on the one hand and to certain marine and brackish-water forms on the other points to it as a link between the marine and fresh-water calanoids. That the genus as a whole has its closest ecological connection with the sea and that it is not a migrant from fresh water to the sea is suggested by the fact that the species are found in marine bays, estuaries, lagoons or ponds along marine coasts where there are direct permanent or more or less recurrent connections with the sea.

Pseudodiaptomus euryhalinus is the latest species to be described (Johnson, 1939) and is of considerable interest in being the only known species on the west coast of North America north of the Panama region from whence Marsh (1913) discovered the first East Pacific species, *P. culebrensis*. Eight other species of the western hemisphere occur on the east coast of North, Central, and South America (Wright, 1937). The remaining 20 or 21 species occur on coasts of Asia and Africa, but none are found in Europe.

The systematic relationships of the species of *Pseudodiaptomus* have been discussed especially by Burckhardt (1913), and for American species by Wright (1936, 1937). The American species are considered to fall into two major groups based on the structure of the fifth feet of the male. One group is represented by a single species, *P. gracilis*, which lacks both endopods in the fifth feet. The second, called the *americanus* group, includes *P. americanus*, *P. coronatus*, *P. pelagicus*, *P. richardi*, *P. acutus*, *P. marshi*, and *P. culebrensis*, all of which possess the endopod on the left fifth foot. *P. cristobalensis* is not discussed, for want of detailed information on structure of the female.

According to this scheme, *Pseudodiaptomus euryhalinus* would fall into the *americanus* group and in the subdivision represented by *P. marshi* of the Atlantic coast of South America and *P. culebrensis* of the Pacific coast of Panama for in agreement with these two closely related species, it possesses a nonarticulated process projecting from the distal posterior portion

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[1] Contributions from the Scripps Institution of Oceanography New Series No. 421.

of the first exopod segment of the right fifth foot. This subgrouping, however, is not entirely clear since according to figures of other species of the *americanus* group the process is represented by a spine more or less fused to the segment. From the geographical position of *P. euryhalinus* one might expect the closest affinity with *P. culebrensis*, but this is not clearly borne out, for the similarity to *P. marshi* appears, from present information, to be somewhat greater than to *P. culebrensis*.

As in *P. marshi*, the female first antennae have 21 segments, the caudal rami are nearly symmetrical. In *P. marshi*, two of the three urosomal segments, the second and third, are indistinctly divided, while in *P. euryhalinus* the urosome consists of only two segments in the adult. Two full egg-sacs are formed by both species, but the genital segments are very different.

P. culebrensis possesses first antennae of 22 segments; the urosome has three distinct segments; the caudal rami are asymmetrical and one of the egg-sacs is reduced.

The fifth feet of the male of *P. euryhalinus*, while on the same general pattern as the other two species, are so different in detail that comparisons cannot readily be made.

The present detailed study of the developmental stages was undertaken in hope that it might aid particularly in deciphering the systematic position of the genus, and in providing information needed in studies that might follow on the biology of the species.

The assistance of J. Bennet Olson in drawing of copepodid stages is gratefully acknowledged.

PROCEDURE

The larvae and early copepodid stages used in the present study were obtained in laboratory cultures reared from adult animals collected in September from the plankton in a saline lagoon in Soledad Creek bed at the immediate sea coast a few miles north of La Jolla, California. Water from the lagoon and also from the open sea taken from Scripps pier were used in culturing, and while the latter appeared to give good results, only the larvae hatched in the lagoon-water were used for study. Both living and preserved animals were studied and comparisons were made with larval stages collected in the lagoon and in the upper reaches of San Diego Bay and in Mission Bay, California.

All drawings were made with the aid of a camera lucida.

THE LIFE HISTORY OF *Pseudodiaptomus euryhalinus*

The eggs are carried in two usually equal egg-sacs attached to the genital segment of the female. Frequently only one egg-sac is present, since the second sac is apparently often lost in the process of clasping by the male. Unlike some copepods the male has a tendency to continue grasping the female even though spermatophores have been transferred and full egg-sacs developed. Clasping usually begins before the female reaches maturity. The persistent clasping is seemingly the cause of urosomal distortion found in the adults. It was not determined whether or not one mating with transfer of a spermatophore suffices for fertilization of successive batches of eggs as occurs in *Cyclops* and *Diaptomus* (Ewers, 1936) and in certain harpacticoids (Nicholls, 1935; Fraser, 1936; Johnson and Olson, MS).

The eggs hatch in 2 to 3 days after the appearance of the egg-sacs, and the first copepodid stage is reached in about 13 days.

The Nauplius Larvae

There are only five free naupliar stages, since the larvae hatch in what is structurally Nauplius Stage II. The nauplii are roughly cylindrical in cross section, but with a little lateral compression. They are oval in outline, becoming more elongate with each successive stage, but the abdomen is not flexed ventrally as in some calanoid nauplii. The thick oval labrum, beset with small spines, is especially conspicuous in lateral aspect. The appendages are of moderate length and there is a conspicuous eye-spot.

Nauplius Stage II

Body (Figs. 1 and 2). Average 0.16 mm long; posterior end cleft and armed with two very unequal long spines, the right being much the heavier. Just anterior to these there are transverse rows of fine spinules on the ventral surface of the body.

First Antenna (Fig. 8). Three segments, the first with one ventral seta, the second with two ventral setae. The end segment is broad in lateral aspect and is provided with three terminal setae, and one aesthete, and a few short spinules.

Second Antenna (Fig. 13). First basipod with a heavy masticatory blade with a bifurcate tip and a slender spine near its base. Second basipod with one strong spine and two small setae. Endopod of one segment with three terminal and two lateral setae. Exopod with two fused proximal segments and five short distal segments.

Mandible (Fig. 18). First basipod with small rounded process bearing a strong spine. Second basipod with two spines and one seta. Endopod of one segment, the major armature consisting of four strong spines on the inner margin and three terminal setae.

Nauplius Stage III

Body (Fig. 3). Average 0.2 mm long, terminating in caudal armature as in II, but with the heavy terminal spine relatively shorter and with the addition of two smooth flexible sensory setae, each of which issues from the dorsal side at the immediate base of each long terminal spine. In some specimens only one dorsally directed seta was found in which case it always occurred over the heavy spine. It is not clear if this is a variable characteristic or if the opposite seta had been lost.

First Antenna (Fig. 9). As in II, but the terminal segment with 2 dorsal marginal setae and one ventral marginal seta.

Second Antenna (Fig. 14). As in II, but with additional setae and with a total of seven exopod segments.

Mandible (Fig. 19). No important change.

First Maxillae (Fig. 3). These appendages are each represented by only a single strong spine.

NAUPLIUS STAGE IV

Body (Fig. 4). Average 0.25 mm long; no change in caudal armature.

First Antenna (Fig. 10). As in III, but end segment with four dorsal marginal and three ventral marginal setae; there is a row of spinules on the second segment.

Second Antenna (Fig. 15). The only significant change other than addition of regular setae is the transformation of the masticatory blade into a coventional type masticatory hook.

Mandible (Fig. 20). The rounded process on the first basipod has been transformed into a strong molar process with a lateral spine.

First maxilla. Rudimentary.

NAUPLIUS STAGE V

Body (Fig. 5). Average 0.28 mm long; caudal armature as in IV.

First Antenna (Fig. 11). As in IV, but with six dorsal marginal and four ventral marginal setae.

Second Antenna (Fig. 16). As in IV.

Mandible (Fig. 21). As in IV.

First Maxilla. Rudimentary.

Second Maxilla. Represented by a strong spine just posterior to the first maxilla.

PLATE I

Pseudodiaptomus euryhalinus

FIG. 1. Nauplius Stage II—ventral (Stage I is passed within the egg).
FIG. 2. Nauplius Stage II—lateral outline.
FIG. 3. Nauplius Stage III—ventral.
FIG. 4. Nauplius Stage IV—ventral.
FIG. 5. Nauplius Stage V—lateral.
FIG. 6. Nauplius Stage VI—lateral.
FIG. 7. Nauplius Stage VI—ventral.

ABBREVIATIONS: a1, first antenna, a2, second antenna; m, mandible; mh, masticatory hook; mx1, first maxilla; mx2, second maxilla; mxp, maxilliped; p1, first pair feet; p2, second pair feet; ss, sensory setae; ts, terminal spines.

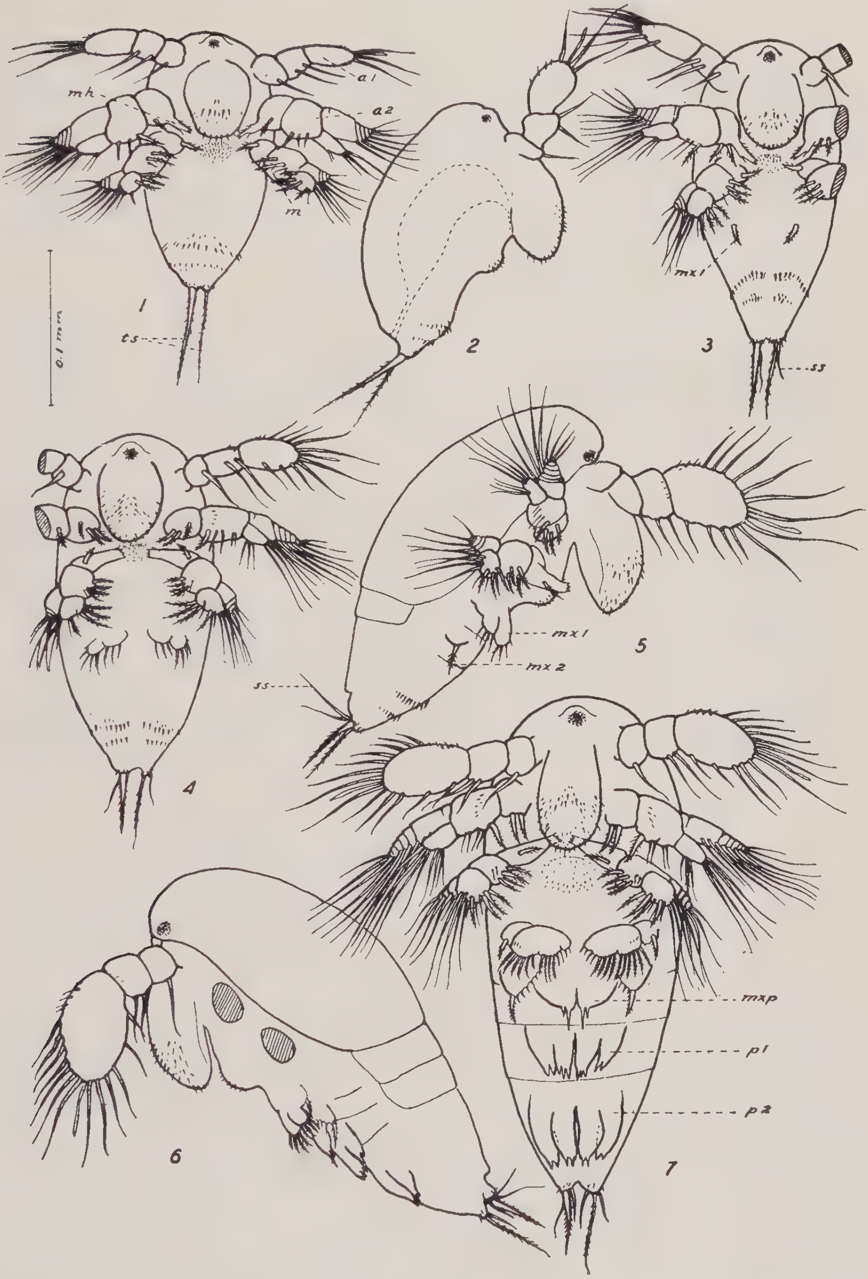
a1
mh
a2
m
1
ts
0.1 mm
2
3
mx1
ss
4
5
mx1
mx2
ss
6
7
mxp
p1
p2

Plate I

NAUPLIUS STAGE VI

Body (Figs. 6 and 7). Average 0.33 mm long; the caudal armature now consists of the two long terminal spines, two dorsally directed smooth sensory setae, and two new smooth sensory setae issuing, one each from near the inner base of the terminal spines.

First Antenna (Fig. 12). Setae as in V, but the terminal segment which has been broadened with each stage is now broader than the combined length of the first and second segments.

Second Antenna (Fig. 17). No major changes.

Mandible (Fig. 22). As in V.

First and *Second Maxilla* (Fig. 7). Rudimentary.

Maxillipeds. Rudimentary.

First and *Second Feet.* Rudimentary.

THE COPEPODID STAGES

The sixth nauplius stage terminates in a critical molt from which emerges the first of six copepodid stages, the last of which is the adult. (See Johnson, 1939 for full description of both sexes.)

In the natural habitats there appears to be a strong tendency for the adult and later copepodid stages to remain near the bottom.

The various stages are readily separated on the basis of body segmentation and on the number of swimming feet present together with their degree of segmentation. The following size ranges and averages are based on measurement of 6 to 13 specimens for each stage:

Stage I, 0.43–0.46 mm (average 0.45 mm)
Stage II, 0.52–0.58 mm (average 0.56 mm)
Stage III, 0.57–0.69 mm (average 0.64 mm)
Stage IV, female, 0.81–0.85 mm (average 0.84 mm)
Stage IV, male, 0.65–0.67 mm (average 0.66 mm)
Stage V, female, 0.96–0.99 mm (average 0.97 mm)
Stage V, male, 0.71–0.77 mm (average 0.75 mm)

In copepodid Stage I (Fig. 23) the metasome is nearly uniform in width consisting of a long cephalic segment and three thoracic segments; the urosome consists of two segments and short symmetrical caudal rami. In successive stages additional thoracic segments are added as shown in Figures 24 to 27. In the male the urosome segments are increased to three and four successively in the fourth and fifth copepodid stages (Figs. 26 and 27).

The female urosome acquires three segments in the fourth stage and remains thus through the fifth stage (Figs. 28 and 29). However, in the adult stage, not figured here, two segments become completely fused to form the genital segment. The caudal rami are nearly symmetrical in all stages, though often the left ramus is slightly the longer in the female.

The head appendages of copepodid Stage I are shown in Figures 31 to 35. In this stage the first and second feet possess one-segmented rami (Figs.

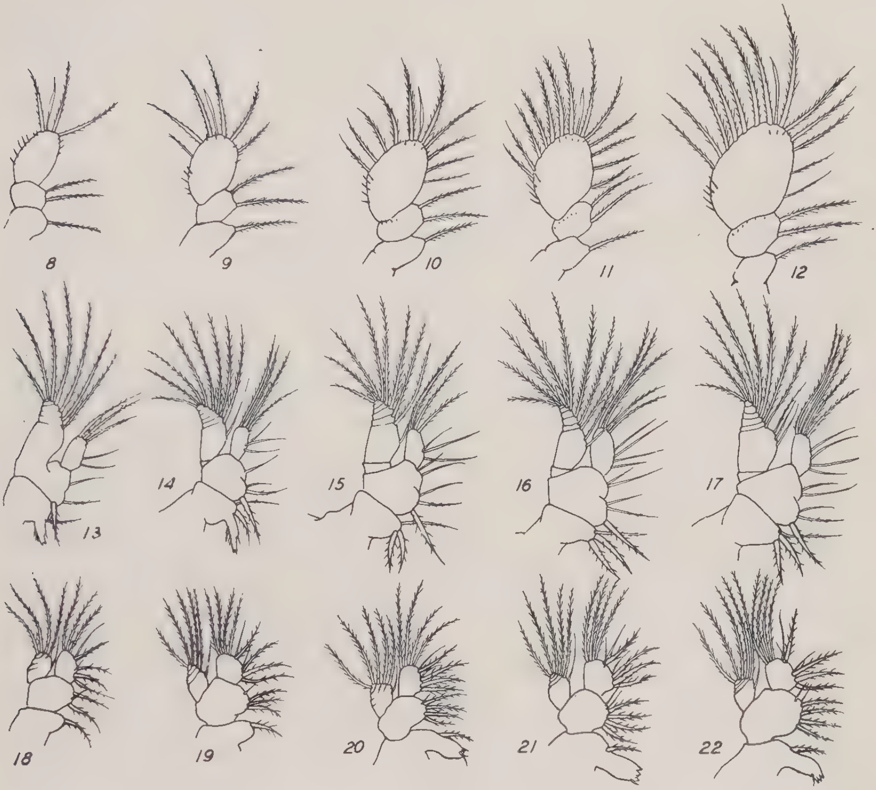

PLATE II

Pseudodiaptomus euryhalinus

FIGS. 8–12. First antenna, Nauplius Stages II–VI.
FIGS. 13–17. Second Antenna, Nauplius Stages II–VI.
FIGS. 18–22. Mandible, Nauplius Stages II–VI.

36 to 41), and the third feet are rudimentary. In succeeding stages the first four pairs of feet follow the regular copepod pattern of appearance and segmentation, resulting in three-segmented rami in all feet in Stage V as shown in Plate III.

The sexes are first distinguishable anatomically in copepodid Stage IV, when the rudimentary fifth feet of the male are already asymmetrical, the left foot possessing a well-developed endopod. This endopod in Stage V is about as long as the exopod and bears the small sensory seta found in the adult (Figs. 52 and 53). In Stage V the right fifth foot of the male possesses a rounded knob on its inner side at the distal end of the penultimate segment. The tissue beneath the chitin sometimes appears to be more or less separated from the basipod, suggesting that the growth may be a retarded endopod. On the other hand it may be the beginning of the elongated process on the first exopod in the adult male. No endopods develop at any time in the female fifth feet which remain symmetrical throughout (Figs. 46 and 47). In Stage V the right first antenna of the male shows the beginning of geniculation (Fig. 30).

DISCUSSION

It is highly probable that the structure of the nauplius larvae of *Pseudodiaptomus euryhalinus* is typical of this interesting genus, for it has been shown in other studies that the larvae of different species of a given genus or of closely related genera show only small variations (Johnson, 1934, 1935) and in some *Diaptomus* species the larvae are said to be indistinguishable (Gurney, 1931).

When comparing the nauplius larva of the present species with the known larvae of other copepods, the closest affinity appears to be with *Diaptomus* though there are a number of important discrepancies. A somewhat more remote similarity is found also to *Heterocope weismanni* and to the genus *Eurytemora*. The body shape is like that of the first two genera (Dietrich, 1915; Gurney, 1931; Ewers, 1930; Elster, 1932) and is apparently similar also to *Eurytemora* as shown by Oberg (1906) and Davis (1943). In common with *Diaptomus* and *Eurytemora* the terminal segment of the first antenna is unusually broad and with full number of well developed dorsal and ventral marginal setae whereas in *Heterocope* the segment is narrow and setae are weak. The armature of the caudal region bears the stouter terminal spine on the rudiment of the right caudal ramus in agreement with figures by Dietrich (1915) for *Diaptomus vulgaris*, but differs from that species in having much longer terminal spines, especially on the left ramus. The terminal caudal spines of *D. castor* as described by Gurney (1931) and of *D. siciloides* as figured by Ewers (1930) contrast with *Pseudodiaptomus* in that they are very small and equal in length. The delicate dorsally directed caudal sensory setae are simple in *Pseudodiaptomus* whereas in *Diaptomus* they are split at the ends, and are wanting in *H. weismanni*. In the last species in Nauplius Stages III to VI there are present two caudal spines situated one each laterally outside the original pair of terminal spines. These are wanting in the other three genera.

The caudal armature of *Pseudodiaptomus* when compared with that of marine genera, recalls the larvae of *Eurytemora hirundo* in the fourth stage, but lacks the short ventral spines or "hooks" situated just anterior to the terminal spines and which are so characteristic of marine calanoid genera (Oberg, 1906). These hooks are also absent in *Diaptomus* and *Heterocope*.

The masticatory hooks on the first basis of the second antenna give no hint as to relationship. The unusual split process (hook) on this segment in Nauplius Stages II and III appears to be peculiar to *Pseudodiaptomus*.

On the basis of adult structure Herrick (1884) and Herrick and Turner (1895) have called attention to similarities of *Pseudodiaptomus* to the marine genera *Metridia*, *Pleuromamma*, *Euchaeta*, and *Centropages*. The larval stages, are however, for the most part, very unlike *Pseudodiaptomus*.

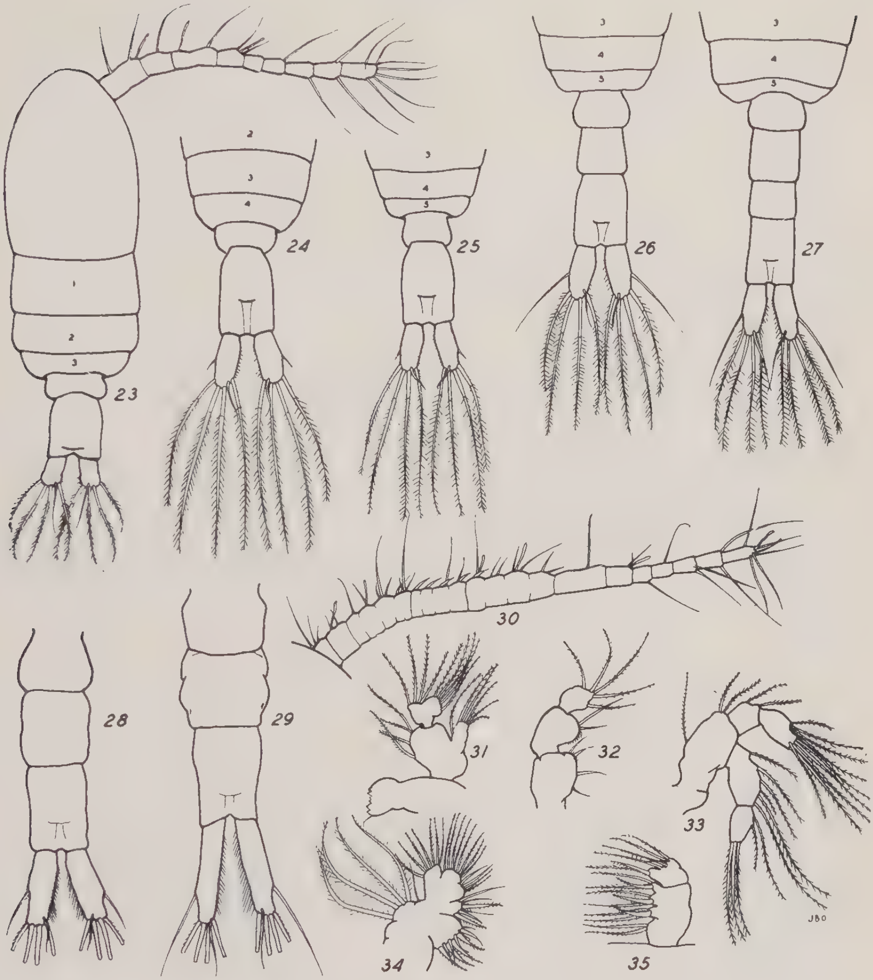

PLATE III

Pseudodiaptomus euryhalinus

FIG. 23. Copepodid Stage I—dorsal.

FIGS. 24–25. Development of urosome and thoracic segments. Copepodid Stages II and III.

FIGS. 26–27. Development of urosome and thoracic segments, male. Copepodid Stages IV and V.

FIGS. 28–29. Development of urosome, female. Copepodid Stages IV and V.

FIG. 30. Right first antenna, Copepodid Stage V, male.

FIG. 31. Mandible, Copepodid Stage I.

FIG. 32. Maxilliped, Copepodid Stage I.

FIG. 33. Second Antenna, Copepodid Stage I.

FIG. 34. First Maxilla, Copepodid Stage I.

FIG. 35. Second Maxilla, Copepodid Stage I.

The larva of *Metridia longa* was described by Gibbons (1938), and is found to be structurally very close to larvae of *Calanus* and *Pseudocalanus*. These three genera differ so markedly from *Pseudodiaptomus*, especially in body shape and caudal armature, that no relationship is suggested.

The larva of *Pleuromamma* appears not to have been identified, but the close relationship of that genus to *Metridia* would seem to eliminate it as well.

The larvae of two species of *Euchaeta* have been investigated by A. G. Nicholls (1934) and Campbell (1934). The large amount of yolk present in the embryo results in a modified nauplius which is not readily compared with other nauplii, but none of its detail structures recall *Pseudodiaptomus*. *Centropages hamatus* on the other hand does show some remote resemblance to *Pseudodiaptomus* especially in body shape and in caudal spines in Nauplius Stage II.

Further comparisons cannot readily be made for want of more detailed study on other species and related genera, especially in the familis Temoridae and Centropagidae. In too many instances the figures of larvae of species already described are inadequate for critical comparisons because of failure to show in detail the differences in relative strength and kinds of spines and processes, especially of the caudal region, and of the first and second basis of the second antennae and mandibles.

So far as the copepodid stages are concerned, the development of *Pseudodiaptomus* is normal for calanoids, and development of the fifth feet is not unusual. Wilson (1932, Fig. 68d) has figured what he calls the fifth pair of feet in the young *Pseudodiaptomus coronatus*, male. The figure, however, agrees so closely with the fifth feet of female Stage V in *P. euryhalinus* that there appears to be an error in labeling Wilson's figure. The absence of an endopod in his figure would then not represent a specific difference in development as it otherwise would, since the adult male of *P. coronatus* does possess a left endopod.

From this study it appears that in so far as the nauplius larva is concerned *Pseudodiaptomus* stands as a well defined genus somewhere between *Diaptomus* and *Eurytemora*, and that it may have its closest *marine* affinities near the latter genus. Ecologically this is in accordance with the notable euryhaline character of *Eurytemora* some species of which range all the way

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PLATE IV

Pseudodiaptomus euryhalinus

Development of the feet

FIGS. 36–40. First foot, Copepodid Stages I to V.
FIGS. 41–45. Second foot, Copepodid Stages I to V.
FIGS. 46–47. Fifth foot, Copepodid Stages IV and V, female.
FIGS. 48–51. Third foot, Copepodid Stages II to V.
FIGS. 52–53. Fifth feet, Copepodid Stages IV and V, male, posterior aspect.
FIGS. 54–56. Fourth feet, Copepodid Stages III to V.

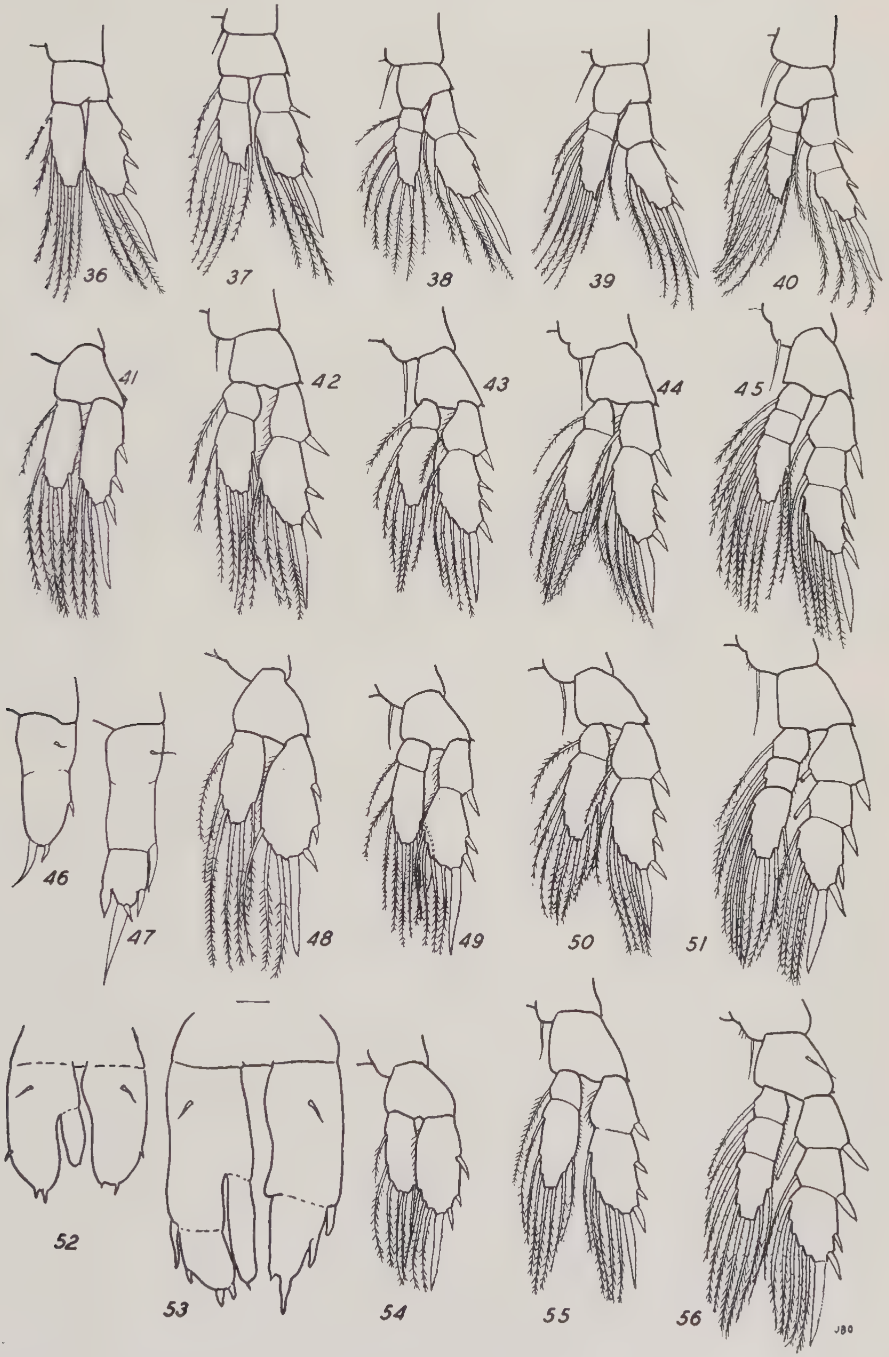
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Plate IV

from marine to fresh water, while a few appear to be confined to water of a specific salinity.

Heterocope is likewise generally considered a brackish-water genus which is found also in fresh and salt water. The caudal armature of its larva appears to be diagnostic for genus but not for family.

The lack of clear family characteristics in the known larvae of recognized copepod families renders the use of larvae as a means of establishing natural relationships extremely difficult.

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THE PREDICTION OF LONGSHORE CURRENTS

J. A. Putnam, W. H. Munk, and M. A. Traylor

(Contribution from the Scripps Institution of Oceanography, New Series, No. 422, and Fluid Mechanics Laboratory Publication No. He-116-279)

Abstract--Longshore currents are an important factor in beach erosion. A relationship is derived from theoretical considerations between the velocity of the longshore current and the height and period of the breaking waves, the angle between the breakers and the beach contours (assumed straight and parallel), and the beach slope in the breaker zone. Field observations and laboratory experiments support this relationship.

Introduction

Waves breaking at an angle with the shoreline set up a longshore current, or littoral current, which may reach a velocity of several knots, and which is capable of carrying large amounts of sediment. If the flow of sediments is impeded, either by direct obstructions in the path of the longshore current, or by interfering with the waves that maintain the current, the equilibrium of the beaches is disturbed, and silting or eroding will follow. A knowledge of the relationship between the character of the ocean waves and the direction and magnitude of the longshore current has proven helpful in the design of jetties and breakwaters.

The impetus for this study came, however, from a different source. During the War, considerable difficulty was experienced in landing amphibious craft in the presence of a longshore current. At times the magnitude of this current was sufficient to cause a landing vehicle to broach, even though it had successfully negotiated the breakers. Often this represented a greater hazard than that afforded by the breaking waves, and it was attempted, therefore, to include a forecast of the longshore currents among the forecast of other characteristics of the surf zone [SVERDRUP and MUNK, 1946].

Field and laboratory observations

Observations of longshore currents were initiated along the beach at Oceanside, California, and simultaneously in the Fluid Mechanics Laboratory of the Department of Engineering at the University of California, Berkeley, California. The results from these studies apply only to straight beaches with parallel contours. It has not been possible to evaluate the effect of currents beyond the breakers, nor the effect of irregularities in the shoreline.

Beach observations--The following wave data were collected each day that measurements were made (see Table 1): breaker height H, wave period T, angle of breaking α, depth of breaking h, mean beach slope m, and velocity of longshore current V. The angle is difficult to obtain, but it can be measured from a pier by standing directly above the breakers and taking a bearing along the breaking crest. Soundings were taken along the pier, and the position of the breakers noted. This was necessary because the beach did not have a regular slope but was characterized by an outer and inner bar. These bars were constantly shifting position, particularly with heavy surf. The wind speed and direction were recorded when the wind was strong enough to be of importance.

Longshore currents were measured by three different methods. Two of these involved the travel time of a current cross over a known distance. The current cross consisted of a sheet metal cross, suspended from a small float, and held upright by a lead weight (see Fig. 1). The line between the float and the cross could be adjusted to measure the current at any desired depth. The damping effect of the wooden braces shown in Figure 1 held the instrument fairly steady in the surf Two types were used, a large cross 16 inches high and a small cross eight inches high, the latter for measurements in shallow water.

The first method was to take an average of several 100-ft runs. One end of a 100-ft line was attached to the current cross and the other to a block of wood which could be lowered from the pier to the water surface by a short line. The cross was dropped into the current, the block was lowered to the surface and then the time required to draw the 100-ft line taut was measured.

Table 1--Tabulation of field data

No.	Date	Time		H	T	α	m	V
	1945	h	m	ft	sec	°		ft/sec
1	Feb. 9	. . . .		5	10	15	0.016	2.5
2	Feb. 21	. . . .		5.5	9	12	0.02	2.2
3	Feb. 24	. . . .		7	9	15	0.023	3.0
4	Mar. 5	. . . .		6	7	7.5	0.017	1.8
5	Mar. 14	10	15	5	10	10	0.031	3.6
6	Mar. 14	13	30	8	10	10	0.022	2.8
7	Mar. 14	14	30	8	10	10	0.023	2.3
8	Mar. 16	10	40	6.5	12	10	0.02	2.4
9	Mar. 16	13	50	4.5	12	10	0.02	2.4
10	Mar. 16	14	45	4.5	12	10	0.019	2.7
11	Mar. 16	15	10	4.5	12	10	0.019	2.1
12	Mar. 22	. . . .		6.5	15	5	0.016	1.7
13	Mar. 23	. . . .		8	7	17.5	0.022	5.2[a]
14	Mar. 24	10	00	5	8	10	0.03	3.3
15	Mar. 24	10	30	8.5	8	12	0.02	2.5
16	Mar. 27	. . . .		5	15	5	0.026	2.4
17	Apr. 9	09	45	9	8	15	0.019	5.5[a]
18	Apr. 9	11	00	9	8	15	0.019	3.9

[a] Following 22 knot wind blowing within 22° of parallel to coast.

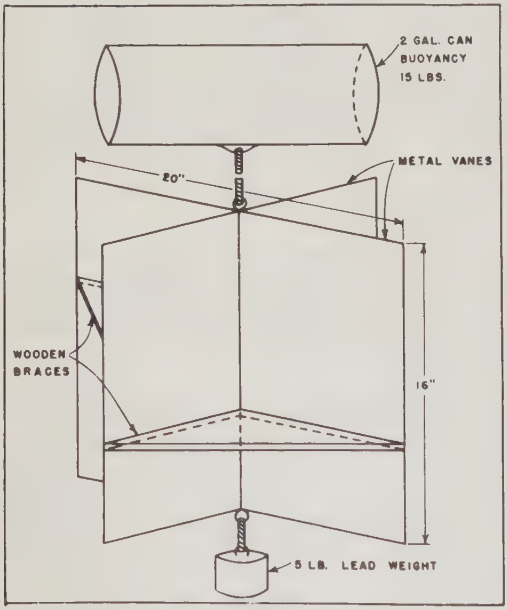

Fig. 1--Current cross used for field measurements of longshore currents

The second method was to drop the cross into the current, either from a boat or from the pier, and to permit it to drift freely. Observers followed along the shore and recorded the time when the cross passed markers at 100-ft intervals until the cross was washed up on the beach, or had drifted out to sea. This method permitted the measurement of currents over long stretches and minimized the effect of errors in timing.

A third method was tried along the beach a few miles north of Oceanside. Fluorescein dye markers were dropped into the current from a low-flying blimp, and were photographed from a plane at five-minute intervals. A party on the beach recorded the wave height and period. On the photographs the progress of the dye could be measured from landmarks along the beach, and the velocity computed. This method has the advantage that breaker angles may be measured directly. However, the diffusion of the dye makes it difficult to determine the exact point of advance. Furthermore, the combination of good flying weather and good waves was so rare that it was more satisfactory to use the other methods.

The surf at Oceanside was usually characterized by a zone of higher breakers on the outer bar, and a zone of lower breakers on the inner bar (see Fig. 2). On days where the majority of waves were breaking on the outer bar, the current was almost constant from the outer line of breakers to shore. During spring tides, however, when only a few of the highest waves were breaking on the outer bar, there would be a weak current between the two lines of breakers, and a strong current between the inner line of breakers and shore. At all times the current was small or negligible beyond the outer breaker.

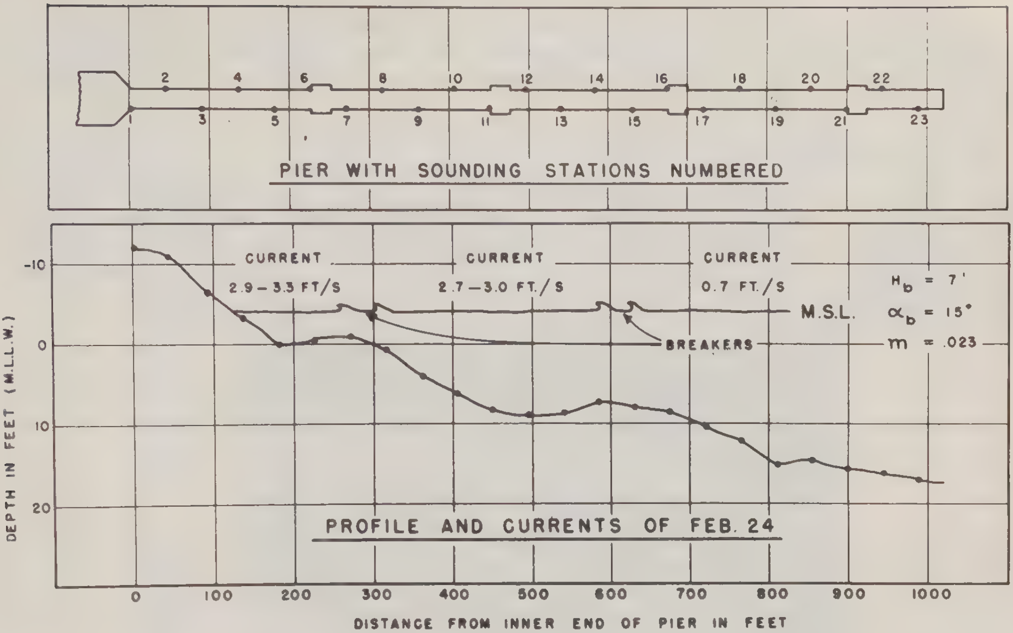

Fig. 2--Typical arrangements for field observations at Oceanside

Along any given stretch of beach the velocity varied as much as 25 per cent either way from the mean value. The observed variations are similar in duration (three to five minutes) to the surges that are observed in rip currents, and are probably associated with the variations in wave height over similar time intervals. Consequently these variations are variations in time, and not in position. This is clearly borne out by observation from a blimp of the movement of six dye markers at different parts of the Oceanside beach (see Fig. 3). In this figure the velocities of markers (1) and (2) were high between runs 1 and 2, and low between runs 2 and 3 (in the case of marker (1) the velocities were low between runs 2 and 4. The velocities of markers (4), (5), and (6) were high between runs 3 and 4, and low between runs 4 and 5.

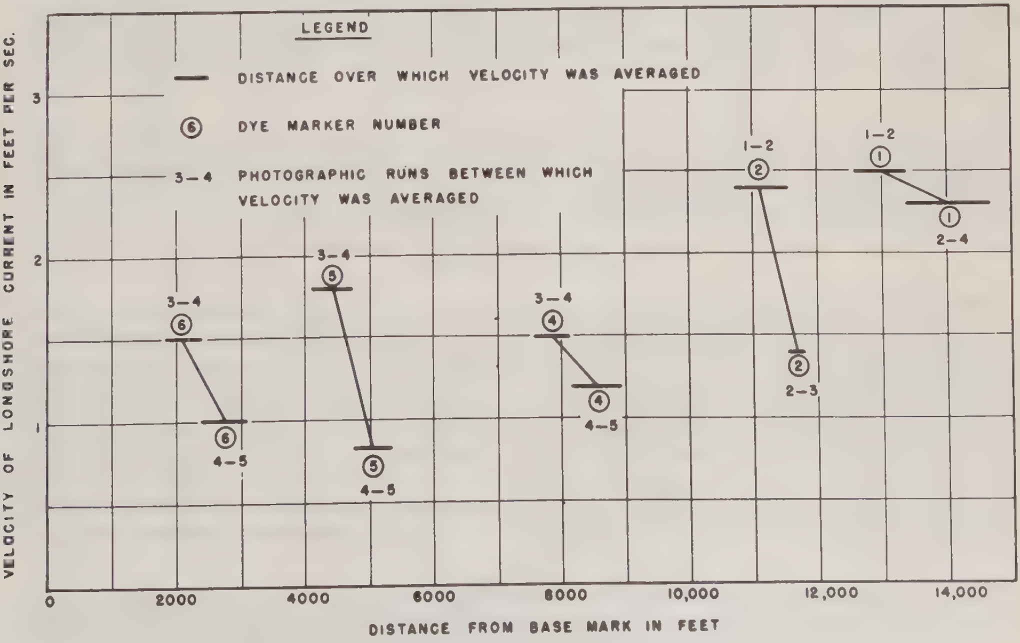

Fig. 3--Movement of dye-markers photographed from a blimp

When waves break nearly parallel to a coast, strong rip currents are set up. These currents run parallel to the beach for a short distance, and then out to sea. They reach velocities up to 1.5 knots. All cases where rip currents were predominant have been eliminated from this investigation.

Laboratory observations--The experimental equipment consisted of a concrete wave basin approximately 58 ft long, 39 ft wide, and two feet deep. Waves of any desired frequency were generated with a motor-driven flap, hinged at the bottom, and located at one end of the tank. At the opposite end of the basin, beaches of any desired slope and angle to wave direction were constructed (see Fig. 4). Beaches of three different absolute roughnesses were used in the investigation. The smoothest beaches were covered with metal sheets or very smooth neat cement. Intermediate roughness was obtained with natural sand bonded with cement to prevent erosion. The roughest beaches were coated with 1/4-inch pea gravel and bonded with a thin grout.

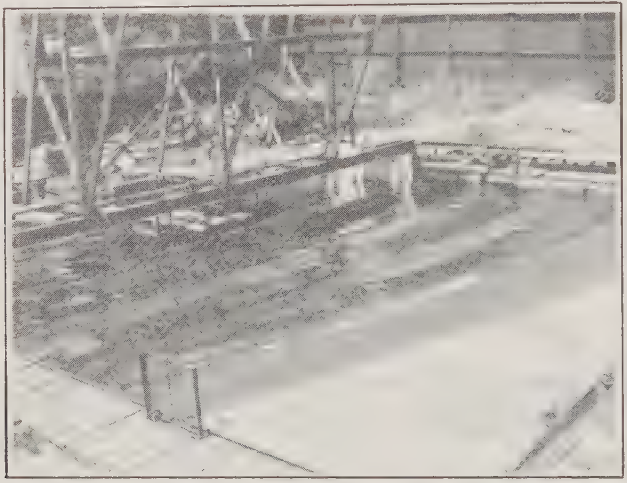

Fig. 4--Laboratory wave basin

Wave heights, breaker heights, and the depth of breaking were measured with electric point gages. Wave periods were obtained by observing the frequency of the wave-generation flap. The angle of the breakers was measured from vertical photographs. The longshore current was measured by timing the travel of KM_nO_4 dye over each five-foot interval marked along the beach. A careful review of the data indicated that measurements of longshore current along different sections of the central position of the beach (five to 15 ft in Figure 4) were consistent and reproducible.

The experimental results are presented in Table 2. All values represent the average of at least three separate determinations. For all runs reported, the length of the beach was ten or more times the width of the surf zone, and all waves broke well inside the toe of the beach slope. Figure 5 illustrates typical surf conditions in the laboratory experiments.

Analysis of the data

The longshore current is a stream which receives energy from the breaking waves. Equilibrium conditions prevail when the fraction of the energy received (available to maintain the longshore motion) equals the rate of dissipation of mechanical energy by friction. An exact analysis is rendered difficult because only a small portion of the wave energy is applied to the maintenance of the current. Although a correlation of the observed data can be obtained by intuitive reasoning based on kinematical considerations or by dimensional analysis, it is believed that relations derived from mechanical principles will yield a better understanding of the phenomenon and also provide a better basis for forecasting longshore currents. Accordingly, two approaches are presented; one based on energy balance, and the other on momentum considerations, both assuming that waves have been breaking long enough to set up a steady state, and that the beach is straight, and the bottom slope uniform.

Energy approach--Consider a volume of water ABCDE (see Fig. 6) extending between shore and the breaking waves, from the surface to the bottom. Over a width of beach dx the total wave energy entering the volume ABCDE equals $C\,E\cos\alpha\,dx$, where C is the wave velocity (almost equal to the

Table 2--Tabulation of laboratory data and results

No.	Aver. K	Slope m	Breaker conditions					Longshore velocity V	
			T	H	h	α	$(mH^2/T) \sin 2\alpha$	Calc.	Obs.
			sec	ft	ft	°		ft/sec	ft/sec
1	0.0397	0.066	1.00	0.47	0.75	18.3	0.205	1.21	0.78
2	0.0397	0.066	1.06	0.32	0.44	13.8	0.143	0.74	0.64
3	0.0397	0.066	1.14	0.40	0.56	14.6	0.166	0.87	0.82
4	0.0397	0.066	1.15	0.31	0.41	12.6	0.133	0.66	0.68
5	0.0397	0.066	1.25	0.30	0.39	11.7	0.124	0.59	0.76
6	0.0397	0.066	1.32	0.32	0.40	11.7	0.127	0.61	0.75
7	0.0397	0.066	1.40	0.29	0.37	10.9	0.114	0.54	0.64
8	0.0397	0.144	1.90	0.16	0.24	17.6	0.104	0.58	0.75
9	0.0397	0.144	2.13	0.15	0.23	17.2	0.095	0.55	0.66
10	0.0397	0.144	2.22	0.15	0.24	17.3	0.094	0.55	0.50
11	0.0397	0.241	0.72	0.28	0.48	18.2	0.250	1.27	1.33
12	0.0397	0.241	0.92	0.35	0.52	16.5	0.260	1.24	1.27
13	0.0397	0.241	1.14	0.22	0.28	10.4	0.154	0.60	0.53
14	0.0397	0.241	1.22	0.22	0.27	10.6	0.151	0.60	0.69
15	0.0070	0.100	0.99	0.24	0.32	28.0	0.169	1.65	1.68
16	0.0070	0.100	1.32	0.22	0.27	22.8	0.138	1.20	1.45
17	0.0070	0.100	1.63	0.16	0.23	18.8	0.099	0.96	0.96
18	0.0070	0.100	1.98	0.16	0.22	18.4	0.092	0.85	0.76
19	0.0070	0.139	0.83	0.28	0.43	56.6	0.234	3.03	2.46
20	0.0070	0.139	0.91	0.23	0.33	45.3	0.201	2.35	2.31
21	0.0070	0.139	1.00	0.22	0.29	38.8	0.187	2.06	2.22
22	0.0070	0.139	1.12	0.20	0.24	33.2	0.166	1.69	1.93
23	0.0070	0.139	1.35	0.20	0.25	31.1	0.154	1.58	1.52
24	0.0070	0.260	0.80	0.34	0.62	57.5	0.324	3.97	3.78
25	0.0070	0.260	0.90	0.29	0.43	52.5	0.286	3.26	3.34
26	0.0070	0.260	0.98	0.28	0.41	47.2	0.275	2.99	3.00
27	0.0070	0.260	1.23	0.20	0.26	32.5	0.197	1.82	1.91
28	0.0070	0.260	1.27	0.22	0.23	31.9	0.207	1.78	1.76
29	0.385	0.098	0.95	0.26	0.36	30.1	0.182	0.52	1.03
30	0.385	0.098	1.33	0.21	0.27	21.4	0.130	0.31	0.46
31	0.385	0.098	1.67	0.16	0.20	18.0	0.096	0.22	0.20
32	0.385	0.098	1.99	0.12	0.19	16.4	0.072	0.17	0.15
33	0.385	0.143	1.08	0.33	0.47	30.4	0.232	0.69	1.32
34	0.385	0.143	1.36	0.29	0.38	24.6	0.188	0.52	0.63
35	0.385	0.143	1.58	0.20	0.27	19.3	0.131	0.33	0.36
36	0.385	0.143	1.91	0.20	0.26	18.4	0.121	0.30	0.32
37	0.385	0.143	2.32	0.22	0.30	19.1	0.122	0.30	0.18

1-14 (Lab. 1), natural-sand beach; 15-28 (Lab. 2), beach covered with sheet metal or smooth cement; 29-37 (Lab. 3), beach covered with 1/4-inch pea gravel.

group velocity for breaking waves), E is the mean energy per unit surface area of the breaking waves, and α is the angle formed between the breaking crest and the shoreline. Of the energy that advances parallel to shore $(C\ E \cos\ \alpha dx) \sin \alpha$, a small fraction s is responsible for setting up longshore currents. The greater part of the wave energy entering this volume is destroyed in the breaker and turned into heat, or may be responsible for piling water against the shore and setting up rip currents.

Energy is dissipated in a layer of frictional resistance along the bottom. The frictional force per unit width of beach equals

$$k \rho V^2 \ell' dx \dots\dots\dots\dots\dots\dots\dots\dots (1)$$

and the rate at which energy is dissipated in the volume ABCDE equals

$$k\rho V^3 \ell' dx \qquad (2)$$

where k is a friction parameter, depending on the hydraulic roughness of the bottom, V the velocity of the longshore current, and ℓ' the distance along the bottom from shore to breaker line. With good approximation $\ell' = \ell$ (see Fig. 6). If m denotes the average beach slope, and h the depth at which the waves break, then

$$m = h/\ell \qquad (3)$$

Assuming a steady state, all the energy available for longshore currents entering the volume ABCDE due to wave action must equal the loss of energy due to friction

$$sCE \cos\alpha \sin\alpha \, dx = k\rho V^3 \, dx \, h/m \qquad (4)$$

The following relationships derived by the solitary wave theory have been found to apply to breaking waves with good approximation [SVERDRUP and MUNK, 1946; MUNK, 1949].

$$E = (\rho g/L)(4h\,H/3)^{3/2} \qquad (5)$$

$$C = [g(h + H)]^{1/2} = L/T \qquad (6)$$

$$h = 1.28\,H \qquad (7)$$

$$Q = 4h^2 \sqrt{H/3h} \qquad (8)$$

where ρ is the density of water, g the acceleration due to gravity, H, L, and T the height, length, and period of the breaking wave, h the depth of breaking, and, for later reference, Q is the cross-sectional area beneath the profile of a breaking wave crest. Combining (4), (5), (6), and (7) gives

$$V = K[(m\,H^2/T) \sin 2\alpha]^{1/3} \qquad (9)$$

where

$$K^3 = 0.871\,g\,(s/k) \qquad (10)$$

According to (9) the velocity of the longshore current depends upon the breaker height, the wave period, the angle formed by the breakers, the beach slope, and the hydraulic roughness of the beach. The first three parameters can be predicted from weather maps [SVERDRUP and MUNK, 1946]; the latter two remain relatively constant over a given beach.

The above solution applies to a situation in which the waves have been breaking long enough to set up a steady state, and in which the region chosen is far enough from any obstruction on the beach so that a full-strength current is reached. A more general solution has been derived which is not subject to these limitations. From these solutions numerical values have been computed for the duration of the transient state, and for the distance from a breakwater or discontinuity in the beach over which a current must flow to reach its full velocity. Both these values are surprisingly small. A current will build up to an essentially steady state within five minutes of the time a train of waves starts to break on a beach, and will have practically its full value within 200 yards of a breakwater or other obstruction. The short duration time is consistent with observations of three to five minute variations in longshore currents due to the variation of wave height over similar time intervals (see Fig. 3).

Momentum approach--With the breaking of every wave a certain water mass is thrown into motion in the direction of wave propagation. The longshore component of this motion provides the driving force for the longshore current.

Consider again the volume ABCDE (see Fig. 6). Let Q represent the cross-sectional area of a breaking wave crest moving with velocity C, L the length of the breaking wave, α the angle formed by the breaking crest with the shoreline, and ρ the density of water. Then $\rho Q\,C/L$ is the average momentum per unit surface area, and $C(\rho Q\,C/L)\cos\alpha dx$ the mean flux of momentum into ABCDE. The component of momentum flux parallel to shore equals

$$C \sin\alpha (\rho Q\,C/L) \cos\alpha dx \qquad (11)$$

The broken water is quickly slowed down by turbulent friction to the mean velocity V of the longshore current, and eventually expelled from the surf zone, giving rise to a momentum flux outward of

$$V(\rho Q\,C/L) \cos\alpha dx \qquad (12)$$

Fig. 5--Surf-zone on smooth laboratory beach

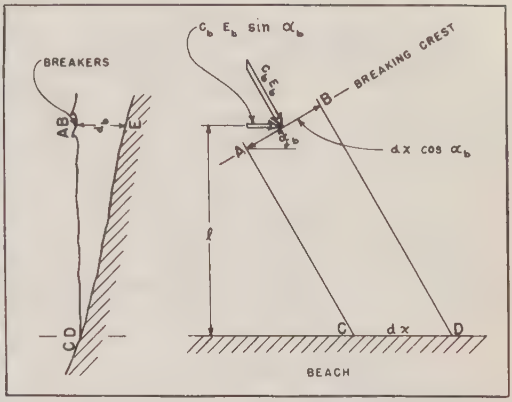

Fig. 6--Schematic diagram for energy and momentum considerations of longshore currents

The difference between (11) and (12)

$$(C \sin \alpha - V)(\rho Q\, C/L) \cos \alpha dx \quad \ldots\ldots (13)$$

represents the net flux of momentum, or equivalent force, applied by the breakers upon the water mass in the surf zone.

Since the longshore current is maintained at an essentially constant rate, this force is balanced by frictional force along the bottom (1). Equations (1), (3), (6), and (13) give

$$V^2 = a\,(C \sin \alpha - V) \quad \ldots\ldots (14)$$

where

$$a = mQ \cos \alpha / khT$$

Solving for V results in

$$V = (a/2)\left[\sqrt{1 + 4C \sin (\alpha/a)} - 1\right] \quad \ldots\ldots (15)$$

where according to (6) and (7) $C = (2.28\ gH)^{1/2}$. Substituting for Q from (8) and using (7) leads to

$$a = (2.61\ mH \cos \alpha)/(kT) \quad \ldots\ldots (16)$$

where, according to (14)

$$k = (2.61\ mH \cos \alpha)(C \sin \alpha - V)/TV^2 \quad \ldots\ldots (17)$$

Equation (15) gives the velocity of the longshore current as a function of the same variables that appeared in (9), and the solution is subject to the same limitations that were discussed when dealing with the energy approach.

Comparison of theory with observed data

In Figure 7 the observed longshore currents are plotted against the wave characteristics as they appear on the right side of (9). Average values of the friction parameter k were determined by substitution of the observed data in (17) for the various types of beach surface investigated. Except for the roughest beach, it was possible to draw a straight line through each set of data, the slope of which is the proportionality constant K of (9). Table 3 illustrates the order of magnitude of the energy fractions available for maintenance of longshore currents, as obtained from (10).

The beach at Oceanside and the natural-sand beach in the laboratory (Lab. 1) have values of s that are comparable. The sand-surface textures of these two beaches were comparable, but the values of the friction parameter k differ by five-fold. A part of this difference may be ascribed to the fact that the beach at Oceanside possessed bars whereas the laboratory beach was a plane,

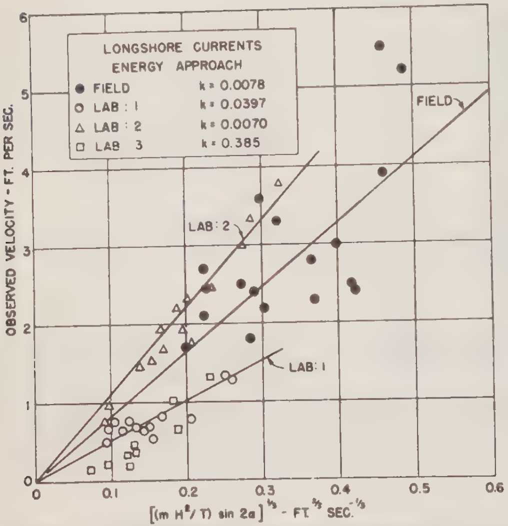

Fig. 7--Longshore currents based on energy approach

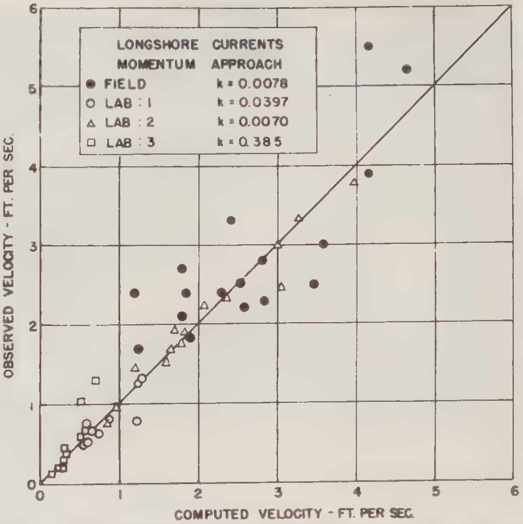

Fig. 8--Comparison between observed and calculated velocities of longshore currents based on momentum approach

Table 3--Values of parameters for field and laboratory data

Beach	k	K	s
Field	0.0078	8.2	0.15
Lab 1	0.0397	5.12	0.19
Lab 2	0.0070	11.02	0.33
Lab 3	0.385	. . . .	. . .

undisturbed surface. However, k depends upon the hydraulic roughness of the beach rather than the absolute roughness of the beach surface. The experiments with the Lab 1 beach were characterized by relatively weak longshore velocities so that viscous forces were relatively large. Thus the higher values of k might be ascribed to boundary layer resistance in contrast to resistance governed solely by roughness. On the other hand, the Lab 2 beach (sheet metal or smooth concrete) was the smoothest one investigated and the values of k are correspondingly small. However, the longshore velocities were in general larger even than those encountered at Oceanside so that it offered less resistance to flow and was therefore able to absorb a larger fraction of the available energy as indicated by the large value of s.

The scatter of the data shown in Figure 7 results primarily from the difficulty of measuring the breaker angle α, both in the laboratory and the field. The very rough beach (Lab 3, 1/4-inch pea gravel) showed a particularly wide range in the individual values of k, from 0.07 to 1.2, and these depended in a systematic fashion upon the longshore velocity. In this case the theory cannot assume a constant average value of k.

Figure 8 shows the observed longshore current plotted against values of the current computed according to (15) using the above average values of k. The agreement of these results indicates that the theory employed is essentially correct.

Conclusion

The laboratory investigation corroborates the field data and the theory, but indicates the need for systematic work, such as has been done in the case of pipe flow, in order to correlate the friction parameter with measureable beach and wave characteristics. Meanwhile, reasonable computations of longshore currents may be obtained by using either (9) or (15) with a value of k taken equal to that obtained from the Oceanside data. Equation (15) has the advantage that no assumption has to be made regarding the selection of the energy fraction available.

The relationships derived here may find application in two ways: (a) in the prediction of longshore currents on the basis of the predicted values for the height, period, and direction of the breaking waves; (b) in the computation of the seasonal variations in the magnitude and direction of longshore currents at chosen localities, on the basis of climatological wave data [BURT and SAUR, 1948]. The restriction to straight beaches with uniform bottom topography greatly limits the usefulness of these applications.

Acknowledgments--This work represents results of research carried out for the Office of Naval Research, the Hydrographic Office, and the Bureau of Ships of the Navy Department under contract with the University of California. We are indebted to Ralph E. Jentoft, Jr. for his assistance in carrying out the observations while on wartime duty at the Scripps Institution.

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The Seminal Vesicles and Testes of *Gillichthys*, a Marine Teleost[1]

By GEORGE F. WEISEL

GLANDULAR structures accessory to the testes of some fish have received scant attention. So-called seminal vesicles were noted as early as 1824 by Rathke in *Gobius niger*. The double seminal vesicles of *Mullus barbatus, Gobius jozzo, G. minutus, G. panganellus* and the single vesicle of *Cobitis fossilis* were briefly described by Hyrtl (1850). An excellent study of the sexual organs of several species of gobies and blennies was made by Eggert (1931). He reported in detail the structure and histology of the seminal vesicle of *Periophthalmus chrysospilos*. In *Esox lucius*, Disselhorst (1904) recognized similar structures, but only in large males during spawning time. Gilbert (1943) gave an account of the seminal vesicles of *Chlamydoselachus*.

The male mudsucker, *Gillichthys mirabilis*, has well developed accessory sex organs. Although this fish is common in the bays and estuaries along the Pacific coast of the United States, the testes and vesicles have not been previously described. This report also includes observations on the seasonal changes in the testes and vesicles, the possible function of the vesicular fluid, and the response of the vesicles to testosterone.

MATERIALS AND METHODS

To determine the seasonal changes in their reproductive tracts, mature male mudsuckers were collected near San Diego, California, in February, March, April, May, August, September and November. The genital papillae were measured across their greatest length and width with a micrometer in the ocular of a dissecting microscope. The testes and seminal vesicles were fixed in Bouin's and after sectioning were stained with hematoxylin and eosin. Some of the sections were also stained with iron hematoxylin or Mallory's triple connective-tissue stain.

STRUCTURE OF THE SEXUAL ORGANS

The male sexual organs of *Gillichthys* consist of the paired thread-like testes, the spermatic ducts, the seminal vesicles and the urogenital papilla.

For the size of the fish (the adults average about 12 cm. in length), the testes are very small. Even during the spawning season they rarely exceed 2 mm. in diameter. The cysts of maturing germ-cells and the spermatozoa are contained in thin-walled lobules. The lobules are usually fused near their bases, where they open into the spermatic duct (Fig. 1), but the distal ends are free. Two to six lobules may lie laterally in the longitudinal series.

In comparison with many teleosts, *Gillichthys* has a simple type of testis. The lobules are simple sacs with few or no trabeculae, instead of the complex network as found in the perch (Turner, 1919), *Cottus* (Hann, 1927), the poeciliids (Geiser, 1921; Vaupel, 1929; Matthews, 1938) and the Pacific salmon (Weisel, 1943). The lobules project individually from the spermatic duct, rather than being bound tightly together by the connective tissue sheath. The walls of the lobules are covered with peritoneal epithelium, which continues dorsally and secures the testis and spermatic duct anteriorly to the air bladder and posteriorly to the kidneys. The lobule walls consist principally of connective tissue fibers. Through this tissue course the capillaries which evidently arise from the main testicular vessels that run parallel with and in the wall of the spermatic duct. No interstitial tissue was found, such as Eggert (1931) described for a related species, *Gobius auratus*.

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The lobules empty directly into the spermatic duct which lies dorsal to them. The duct is generally single. It is lined with cuboidal or squamous epithelium. The surrounding layer of connective tissue and smooth muscle is thicker than that of the lobular walls. At its posterior extremity the duct from each testis enters a common pore in the genital papilla.

The spermatic duct has ventrally projecting lobules for its entire length until it reaches a position ventral to the urinary bladder. At this point there arises the comparatively large fanshaped seminal vesicle (Fig. 2). This organ has the appearance of greatly enlarged lobules which contain a bright yellow fluid rather than the milky substance of the testes. The anterior lobes of the vesicle seem to be a graduation from the testicular to the vesicular lobules. Serial sections prove that there is such a transition. The epithelium lining the lobules in this transitional zone is partially secretory and partially germinal. Beneath the peritoneum, which covers the external surface of the vesicle, lies a thin layer of connective tissue and smooth muscle. The connective tissue layer is heaviest at the basal portion, where the ducts of the seminal vesicle are in direct communication with the spermatic duct. The larger blood vessels are in this region. The layer of connective tissue becomes progressively thinner toward the distal end of the vesicle and contains only small blood vessels.

The internal surface of the vesicle is covered with a continuous epithelium. The epithelial cells are undoubtedly secretory. Their appearance conforms with the excellent description given by Eggert (1931) for the seminal vesicles of *Periophthalmus chrysospilos*. Eggert distinguished two types of secretory cells in the vesicles of *Periophthalmus*. My observations revealed only one type in *Gillichthys*, and the vesicular fluid contains no discrete droplets. The species of *Gobius* investigated by Eggert likewise produce only one type of secretion.

When the cavities of the vesicles are distended with fluid the epithelial cells are squamous. In vesicles which contain little or no fluid the epithelium is mostly cuboidal to columnar. The cells lining the base of the vesicular lumen are more columnar than are those in the distal end. The nuclei are generally basal and only infrequently centrally located. Eggert believes that secretion occurs principally in the distal and central portion of the vesicle. My observations agree with those of Eggert.

With the exception of a few spermatozoa found at the base of the seminal vesicle, where it joins with the spermatic duct, and in the transitional lobules, spermatozoa are not found in the vesicle. At these locations the spermatozoa and the vesicular fluid are mixed, but the organ undoubtedly never serves for the storage of spermatozoa.

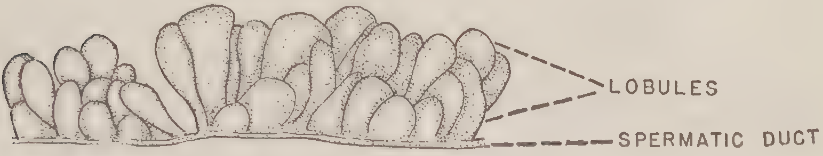
LOBULES
SPERMATIC DUCT

Fig. 1. Detail of a portion of testis of *Gillichthys*.

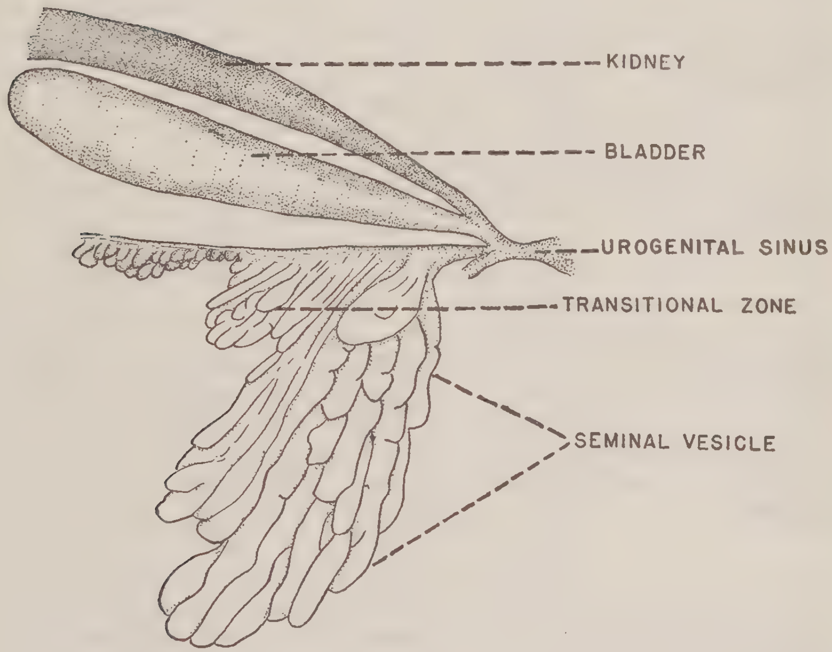
KIDNEY
BLADDER
UROGENITAL SINUS
TRANSITIONAL ZONE
SEMINAL VESICLE

Fig. 2. Detail of the "seminal vesicle" and related urogenital system of *Gillichthys*.

Seasonal Changes

The seasonal changes in the vesicle were determined and were correlated with the condition of the testes. Particular effort was made to obtain males of the same size at different months for such a study. Examination of ovaries and young had already shown that *Gillichthys* has a long breeding period, ex-

TABLE I

SEASONAL CHANGES IN THE TESTES AND THE "SEMINAL VESICLES"

Date	Average Standard Length in cms.	Condition of Testes			Average Widths of Vesicular Lumen in mms.†
		No. Fish	Cysts of Spermatogonia & Spermatocytes*	Spermatozoa	
Feb. 28, '46 Early spawning period	11.4	1	medium	few	0.27
		1	few	full	0.35
		3	none	full	0.25 (av.)
		5			0.29
April 5, Mid-spawning period	11.8	1	few	full	0.36
		1	few	few	0.10
		2			0.23
May 18, Mid-spawning period	12.2	4	none	full	0.32 (av.)
		1	none	few	0.21
		5			0.27
Aug. 15, Early post-spawning period	12.3	2	medium	few	0.36 (av.)
		1	few	full	0.40
		2	none	full	0.23 (av.)
		1	none	few	0.29
		6			0.32
Sept. 12, Post-spawning period	12.6	4	full	few	0.44 (av.)
		3	medium	few	0.43 (av.)
		7			0.44
Nov. 29, Pre-spawning period	11.6	2	full	few	0.27 (av.)
		6	medium	full	0.29 (av.)
		2	few	full	0.28 (av.)
		10			0.28
March 30, '47 Spawning period of next year	12.3	1	medium	few	0.33
		5	none	full	0.20 (av.)
		3	none	few	0.16 (av.)
		9			0.23

* The number of spermatozoa and cysts of maturing germ-cells was set by qualitative impressions.

† The diameters of the lumen of ten sections from the central portion of the vesicles were measured for each fish.

tending from January to July (Weisel, 1947). Table I summarizes the germ-cell development in the testes and the average widths of the vesicular lumen during the pre- and post-spawning periods as well as for the spawning period.

The testes exhibited a definite seasonal cycle, but there were no sharp changes. Some spermatozoa were present in the testes the year around and spermatogenesis was continuous. At the height of the spawning period (March, April and May) the testes and spermatic ducts were packed with spermatozoa and had very few or no cysts of spermatocytes and spermatids. It was assumed that the act of spawning had just been completed in several individuals taken during these months as their testes had only a few spermatozoa in the lumen of their ducts and lobules. The spermatozoa were few but the lobules were filled with cysts of maturing germ-cells in the post-spawning period in September. Some of the testes from fish taken in August showed this condition whereas others were like those in the spawning months. By the last of November, which is in the pre-spawning period, the spermatozoa again increased greatly in number and the cysts of germ-cells decreased proportionately.

Seasonal changes in the seminal vesicles were less evident. Measurements of the epithelial cell heights as an index to secretory activity met with no success. The cell heights varied greatly from the basal to the distal end of the vesicle and even in sections the same distance from the base. A statistical analysis of the measurements taken proved them to be of no significant value. Also, the position of nuclei and the intensity of staining did not show any seasonal differences. The gross and microscopic appearance of the vesicles was the same in the different months except that the amount of fluid was considerably reduced in fish which had, as determined from the examination of their testes, just finished spawning. As a criterion for the amount of fluid in the vesicles, the average width of the lumen was found to be more reliable than the weight of the vesicles. The averages indicate that the vesicles were most distended in the post-spawning month of September and that they contained the least amount of fluid in the spawning months of March and April (Table I), but this circumstance may be attributed to the partial emptying of the vesicles in the latter months by the spawning act. The most distended vesicles of fish which, as judged from the appearance of their testes, had evidently not yet completed their spawning in March or April were no larger than vesicles from post- and pre-spawning fish.

The papillae of the fish in different seasons varied greatly in size, but no indications were obtained of enlargement or other difference that could be correlated with the sexual cycle. The measurements, however, were made on preserved material, which undoubtedly did not fully or reliably represent the conditions in life. I have noticed that the papilla becomes suffused with blood and swollen in gravid females, but this was not observed in the males. Eggert (1931) stated that the papilla of the species of gobies he studied had an erectile tissue.

Response to Testosterone

One of the most notable effects of androgens is on the Wolffian duct and its derivatives (Moore, 1939; Burrows, 1945). The response of the seminal vesicles of *Gillichthys* to testosterone was negative. This lends support to the morphological evidence that the vesicles do not arise from the Wolffian duct and hence are not homologous with mammalian seminal vesicles. Mature male fish were injected intraperitoneally three times at 7-day intervals with 0.8 mg. methyl testosterone (Metandren, Ciba) or were treated by simply adding 5 mg. of powdered methyl testosterone or 8 mg. nonesterified testosterone per 20 liters of their standing aquaria water which was renewed every other day. The fish were killed for examination after 10 to 20 days of treatment. The seminal vesicles from treated fish were similar in weight and in histology to vesicles from control fish.

There is little doubt that androgens induce the nuptial coloration and mating behavior in certain fish (Noble and Borne, 1940; Burger, 1942). Daily observations were made to determine whether the male sex hormones would induce out of season the remarkable fighting behavior and color changes which *Gillichthys* show during their spawning period (Weisel, 1947). Neither fighting nor color changes were noticed. However, *Gillichthys* is a poor subject on which to detect the enhancement of breeding behavior by male hormones. Even during the spawning season, mating behavior occurs only when the mudsuckers are thoroughly accustomed to their tanks and have selected their territories and mates. Also, the black hue affected by *Gillichthys* during their mating is probably due to a nervous control of the chromatophores, as it appears and disappears in a few seconds. It is apparently not the same as the breeding coloration of many other fish, which is assumed gradually and is more or less permanent during the spawning season.

To check potency, the methyl testosterone and nonesterified testosterone samples were successfully tested on *Gambusia* females which had their anal fins clipped. Gonopodia were formed by all. The hormones were added to the water in the same dilutions as they were with *Gillichthys*. This does not deny the possibility that adminstration of larger quantities of the androgens would not have had noticeable effects on *Gillichthys*.

Observations on the Function of the Vesicular Fluid

The function of the vesicular fluid is not known. Reports that it prolongs the life of the spermatozoa after spawning are not confirmed for *Gillichthys*. Eggert (1931) found that spermatozoa teased from the testes of *Gobius panizzae* maintain a lively activity for 30-35 minutes in sea water, but that, if he added vesicular fluid to the sea water, the spermatozoa maintain their activity for at least 50-60 minutes. Eggert concluded that " . . . geht deutlich hervor, dass das Samenblasensekret die Aufgabe besitzt, den Spermatozoen eine längere Bewegungsfägigkeit zu verleihen." Similar experiments were made with spermatozoa of *Gillichthys* by Young and Fox (1937) and by myself (Weisel, 1948). We agree that spermatozoa live as long in sea water as in sea water with vesicular fluid added.

Schlenk and Kahmann (1938) reported that spermatozoa from trout remain immobile until the sperm fluid is diluted, and that it is the potassium in this fluid which prevents movements of the spermatozoa in the undiluted fluid. This does not appear to be the case for the spermatozoa of *Gillichthys*. Spermatozoa from teased testes when placed in hanging-drop preparations of straight vesicular fluid remained inactive. When these same preparations were diluted with sea water or fluid from the coelomic cavity of the fish, the spermatozoa became active immediately. Spermatozoa which had remained inactive in a drop of vesicular fluid for six hours were activated by addition of sea water, and the majority maintained this motility for two hours. Solutions of NaCl, KCl, $MgCl_2$, and $CaCl_2$ with an osmotic pressure similar to sea water activated the spermatozoa lying dormant in the drop of vesicular fluid. These solutions also activated spermatozoa from teased testicular tissue with no vesicular fluid present. Dilutions of vesicular fluid with dextrose solutions which had an osmotic pressure the same as that of sea water also activated the spermatozoa. However, if the vesicular fluid was diluted with fresh water, the spermatozoa were not activated. Consequently, the activating factor of the sea water is not caused by a dilution of any of the vesicular constituents, nor by addition of specific ions in the sea water. Also motility is not induced by reducing the viscosity of the vesicular fluid when fresh water is added. The spermatozoa are not activated by a change in pH since they become motile in solutions ranging in pH from 4.8 to 10.1 (Weisel, 1948). The pH of the vesicular fluid is close to 7.2 (Young and Fox, 1937). It is more likely that activation is caused by change in osmotic pressure (Ellis and Jones, 1939).

It is possible that the vesicular fluid serves to keep the spermatozoa in an inactive state and to nourish them. This would apply only to the comparatively few spermatozoa in the basal chambers of the seminal vesicles as none of the typically staining vesicular fluid was found in the testes proper. Probably the true function of this fluid can only be determined by actual fertilization tests.

Discussion

The seminal vesicles of the gobies are not a part of the Wolffian duct system and are in no way homologous with the accessory male organs of reptiles and mammals (Eggert, 1931). It is evident from morphological examination of the seminal vesicles of *Gillichthys* that they are similar to testicular lobules, but are specialized for secretion. This is clearly indicated in the transitional zone between the testis and the vesicle, where lobules have a mixed germinal and secretory epithelium.

The experiments with testosterone show that the seminal vesicle of the goby is unlike the true seminal vesicle (of mammals) physiologically as well as in embryonic origin. Since it is not a part of the Wolffian duct system, it is not surprising that male hormones do not favor its development.

Accessory sexual organs are more highly developed in the gobies and blennies than in many other types of bony fish. It is possible, however, that the spermatic ducts of many teleosts are secretory and perform the same function as these specialized outgrowths. Fish that possess no vesicle often have spermatic ducts which are tortuous and which are covered with what is apparently a secretory epithelium (Langer, 1913; Lickteig, 1913; Weishaupt, 1925). I have re-examined the spermatic ducts from Pacific salmon, which were used in another study, and find that the epithelium lining the complicated ducts is similar to that of the seminal vesicles of *Gillichthys*.

The presence of an accessory sexual organ in *Gillichthys* may be related to the small size of the testes. The weight of the vesicles far exceeds that of the testes themselves (four fish taken in August with an average body weight of 28.5 gm. had testes which averaged 13.2 mg., whereas the average weight of their vesicles was 32.5 mg.). Possibly the quantity of the spermatozoa can be reduced and fertilization still remain effective due to some action of the vesicular fluid. However, *Gillichthys* spawns in holes in mudbanks where the spermatozoa are less subjected to scattering by currents than are the spermatozoa of most other fish. Hence, the spermatozoa may not be required in such large quantities.

In correlation with the uniform climate in its range, the spawning season of *Gillichthys* is protracted and seasonal changes in the sexual organs are slight. Eggert (1931) concluded from his morphological investigations that the seminal vesicles are secretory and that in the northern species of blennies the secretory activity parallels the ripening of the testes. In *Periophthalmus,* which comes from a tropical climate and which is not a periodic spawner, he found that the secretions are present throughout the year. Although *Gillichthys* is a periodic spawner, the seminal vesicles contain approximately the same amount of fluid and the secretory cells have the same appearance at all seasons. Directly after the act of spawning has been completed, however, the vesicles contain less fluid as it is largely expelled as a constituent of the milt.

SUMMARY

1. The mudsucker, *Gillichthys mirabilis,* has well developed seminal vesicles. These accessory sexual organs are specialized portions of the posterior end of the testes, and are not homologous with the seminal vesicles of higher vertebrates. The function of the vesicle is not known.

2. The vesicular contents maintain the sperm in viable but inactive condition. Activation is probably effected by a change in osmotic pressure. Maintenance of the spermatozoa may be the function of the vesicles.

3. The testes are simple in structure and comparatively very small. The germinal elements are contained in sac-like lobules, each of which empties directly into a dorsal spermatic duct.

4. No seasonal changes were observed in the seminal vesicles. On the average, the height of the epithelial cells and the location of the nuclei seem to remain constant. The vesicles contain most fluid in the post-spawning month of September. The amount of fluid is small during the breeding season because much is expelled by spawning.

5. The testes undergo a seasonal cycle. Except when emptied by the spawning act, the lobules are packed with spermatozoa during the breeding season, January to July. In August and September, cysts of spermatocytes and spermatids increase in number, and few spermatozoa remain in the lumen of the lobules. By November, the spermatozoa for the next spawning period are being produced, and the cysts of germ-cells decrease in number.

6. Methyl testosterone added to the water and injected into the fish and nonesterified testosterone added to the water apparently have no effect on the seminal vesicles. The epithelial cells and the fluid contents remain unchanged. This fact shows that the seminal vesicles of *Gillichthys* differ

from those of higher vertebrates physiologically as well as in embryonic origin.

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MESOZOA OF THE FAMILY DICYEMIDAE FROM CALIFORNIA

BY

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INTRODUCTION

THE DICYEMID MESOZOA are small vermiform organisms that occur in great numbers attached to the renal organs of various cephalopod mollusks. Knowledge of the dicyemids is embodied in several works dealing primarily with species in Europe. Those in America are largely unknown, the only published accounts of them being two short preliminary papers by Wheeler (1897, 1899), two by McConnaughey (1938, 1941), and part of the recent monograph by Nouvel (1947). These works do not constitute an adequate survey of the group.

The present paper is confined to descriptions of the species from the coast of California and Lower California, and to discussion of certain questions relating to classification. Keys to all known species are included to facilitate determination and comparison. A detailed discussion of questions relating to the morphology and life cycle will be given in a later paper.

The writer is especially indebted to Dr. Harold Kirby and the late Dr. S. F. Light of the University of California, under whose direction the work was conducted; to Dr. Martin Johnson, Dr. Dennis L. Fox, Dr. Wesley R. Coe, Dr. Carl Hubbs, Dr. Henry Kritzler, and Mr. Sheldon C. Crane of the Scripps Institution of Oceanography, for aid and suggestions during the course of the study and help in the collection of cephalopods; and to Dr. S. S. Berry of Redlands, California, and Dr. Grace Pickford of Yale University for aid in the determination of cephalopods. Dr. Horace Stunkard kindly read the manuscript and offered numerous helpful suggestions.

MATERIALS AND METHODS

The descriptive studies were based primarily on cover-slip smear preparations from the kidneys of freshly killed cephalopods, fixed in Bouin's fluid and stained with Ehrlich's acid hematoxylin. Living specimens of most of the species have also been studied.

Cephalopods obtained at localities from San Francisco Bay, California, to Rosarito Beach, Lower California, and from the Coronado Islands have been examined for dicyemids. All octopuses taken along the California coast, except one very small one, were infected. The pelagic squid *Loligo opalescens* taken at two stations near La Jolla, California, one about three miles offshore just outside the kelp beds, the other about six miles offshore, showed no infections in a series of sixteen living specimens. A number of specimens of the squid obtained from fish markets in San Francisco and San Diego from time to time also contained no mesozoa. A very few dicyemids were present on some smear preparations kindly sent to the author by Mr. N. Riser of the Hopkins Marine Station, made from a specimen of *Loligo opalescens* taken in Monterey Bay in September, 1947. However, there was insufficient material present from which to make a specific diagnosis. This is the first record of infection of squids from the Pacific coast by mesozoa. A paper nautilus *Argonauta pacifica* from near Cedros Island was free from these parasites.

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In addition, the writer has examined a series of sixteen living octopuses on Oahu Island, Territory of Hawaii, and one on Kwajalein in the Marshall Islands. None of the octopuses from the Central Pacific islands was found to be infected.

DESCRIPTION OF SPECIES FROM THE CALIFORNIA COAST

The dicyemids comprise a total of 31 known species, including 13 from the California coast. They are distributed among three genera as follows:

Genus	Total known species	California species
Dicyemennea	10	7
Dicyema	18	5
Conocyema	3	1

The descriptions and figures refer to the vermiform phases ordinarily seen, the primary and secondary nematogens and rhombogens, except where otherwise indicated. For those species which have not been found along the California coast a brief explanatory paragraph is added to the key, giving their distribution, hosts, and additional points helpful in determination.

Genus Dicyemennea Whitman, 1883

Diagnosis.—Calotte 9-celled; almost always orthotropal; propolar cells 4, 2 dorsal and 2 ventral; metapolar cells 5, 1 dorsal, 2 dorsolateral, 2 ventral; vermiform larvae of most species with abortive second axial cell located anterior to the axial cell proper, in the region of the metapolar cells; this second axial cell usually absorbed shortly after escape of larva from parent nematogen, leaving no trace in adult.

Type species.—*Dicyema eledones* Wagener, 1857.

KEY TO THE SPECIES OF DICYEMENNEA

1. An abortive second axial cell present as a constant feature in inclosed vermiform larvae, just anterior to the axial cell proper.................................2

No abortive second axial cell formed during development of vermiform larva.

A large species often 4 to 6 mm. long, with clear nongranular somatic cells, no verruciform cells; total number of somatic cells 23. Hosts: *Sepia officinalis* Linnaeus and *Sepia orbignyana* Férussac. Distribution: Mediterranean.................................*gracile* (Wagener, 1857)

2. (1) Axial cell ends anteriorly behind or between posterior ends of metapolar cells; calotte conical, extending forward beyond axial cell as a solid body; abortive second axial cell of vermiform larvae not usually farther forward than middle of metapolar cells; cephalic swelling often widest at level of parapolar cells or even farther back; cell number usually variable.................................3

Axial cell extends forward to or between the bases of the propolar cells, calotte fitting over its anterior end in manner of cap or helmet, or taking form of flattened disc at more or less truncated end of body; abortive second axial cell of vermiform larvae well forward near base of propolar cells; cell number constant or variable within small limits 7

3. (2) Medium-sized to large species, adults usually exceeding 1 mm. in length; uropolar cells and sometimes 1 or more diapolars verruciform 4

Small, adults usually less than 1 mm. in length; generally no verruciform cells; total number of somatic cells 21 to 26, commonly 25 .... *abasi* n. sp.

4. (3) Total number of somatic cells 27 to 42, almost always in the thirties; adults mostly 1 to 4.5 mm. long 6

Total number of somatic cells 23 to 29; adults usually 0.5 to 2.0 mm. long 5

5. (4) Somatic cell number usually 24 to 27, sometimes exceeding these limits in either direction; uropolar cells verruciform, others occasionally so; cytoplasmic protein reserves formed as rather large irregularly shaped lightly staining aggregates in somatic cells of trunk, particularly the verruciform cells; diapolar cells of rhombogens sometimes heavily charged with small granules .... *abelis* n. sp.

Somatic cell number usually 23, sometimes higher; uropolar cells and commonly 1 or 2 diapolars verruciform; verruciform cells large, characterized by numerous deeply staining bodies in their cytoplasmic network .... *adscita* n. sp.

6. (4) Somatic cells, except verruciform cells, parapolars, and sometimes the anterior diapolar cells, quite clear in life or lightly granular; body long and slender; total number of somatic cells 27 to 42, almost always in the thirties
.... *californica* McConnaughey, 1941

Somatic cells, except those of calotte and verruciform cells commonly heavily charged with rounded proteinaceous refractile granules giving them an inflated dark appearance in life, axial cell forming a median transparent band; calotte narrower than anterior end of trunk, extending forward from it as a clear conical projection in sharp contrast to the dark heavily granular trunk; total number of somatic cells usually in the low thirties .... *granularis* n. sp.

7. (2) Calotte conical; infusoriform with only 1 free nucleus and 1 germ cell in each cell within the urn; somatic cell number 23 8

Calotte flattened, discoid; propolar cells notably smaller than, and ringed by, the metapolar cells, the 2 groups together forming a flattened disk; infusoriform with 2 nuclei and 1 germ cell in each cell within the urn 9

8. (7) Adults slender, often 5 to 8 mm. long.

A much elongated species, swollen at the anterior end, the parapolar cells subequal to the calotte and taking part in the cephalic swelling; propolar cells much smaller than the metapolars; no verruciform cells. Hosts: *Eledone cirrhosa* (Lamarck), *E. moschata* (Lamarck), and *Octopus saluzzi* Vérany. Distribution: Mediterranean .... *eledones* (Wagener, 1857)

Adults robust, short, less than 2 mm. long.

A small stocky species without verruciform cells, generally widest anteriorly and tapering gradually to the posterior end; somatic cells typically 23, characterized by one or more falciform acidophile proteinaceous rods in each. Hosts: *Octopus vulgaris* Lamarck, and *Eledone cirrhosa* (Lamarck). Distribution: Atlantic coasts of Europe, Mediterranean .... *lameerei* Nouvel, 1932

9. (7) A strong constriction behind the parapolar cells setting off the cephalic swelling from the rest of the body; calotte deeply staining in contrast to the remaining somatic cells; metapolar cells inflated, commonly extending forward around and beyond the propolar cells making the calotte concave; adults usually less than 1 mm. long; total number of somatic cells constant, 25 .... *abbreviata* n. sp.

No strong constriction behind the parapolar cells; calotte flattened but not concave, often obliquely tilted; contrast in staining between calotte and trunk much less marked; total number of somatic cells usually 27
.... *brevicephala* McConnaughey, 1941

Dicyemennea californica McConnaughey, 1941

(Pl. 1, fig. 1; pl. 2, figs. 19–22)

Diagnosis.—Adults usually 1 to 4 mm. long, slender, transparent in life except for the granular contents of the parapolar, anterior diapolar, and verruciform cells; total number of somatic cells variable, from 27 to 42, usually 30 to 39; tendency to segregate into 2 overlapping groups, one with 30 to 34, the other with 35 to 37 (higher numbers exceptional) somatic cells; cephalic swelling composed of the calotte, the parapolar, and the first 2 or 3 diapolar cells, generally broadest at the level of the parapolars; calotte conical, orthotropal; parapolar cells shield-shaped, about equal to the calotte in length or somewhat exceeding it; axial cell extends forward only a short distance between the bases of the metapolar cells, not reaching the propolars; uropolar cells verruciform, other verruciform cells occasionally present.

Vermiform larvae with abortive second axial cell at anterior end of the axial cell between the basal ends of the metapolars; calotte of larvae sharply pointed; larvae elongate, attaining 0.15 to 0.3 mm. before escaping from the axial cell of the parent nematogen.

Rhombogens often slightly longer and broader than nematogens; somatic cells of trunk in this phase commonly with 1 to 5 accessory nuclei of various sizes; axial cell with paranuclei corresponding in number to the number of infusorigens present.

Infusoriform 38 to 45 microns long, rounded posteriorly, each cell within the urn containing 2 nuclei and 1 germ cell.

Host.—*Octopus bimaculoides* Pickford and McConnaughey.

Distribution.—Southern and Lower California.

Types.—Syntypes USNM cat. no. 22682. Paratypes in USNM and in collections of author and of Nouvel.

McConnaughey (1941) stated that the cell number of primary nematogens is 36, that of primary rhombogens 31. This was based on study of insufficient material. Individuals of both phases exhibited variation in cell number over most of the range.

Dicyemennea granularis n. sp.

(Pl. 1, fig. 2; pl. 2, figs. 28–29)

Diagnosis.—Adults usually 1 to 4 mm. long, broad and robust-appearing, often exceeding 100 microns in width; total number of somatic cells 29 to 41, usually 30 to 35; trunk dark-appearing in life owing to heavy accumulation of proteinaceous eosinophilic granules in the somatic cells except those of the calotte, uropolar cells, and any verruciform cells present; calotte conical, orthotropal, generally narrower than the trunk, from which it projects as a clear protuberance; cephalic swelling composed of the calotte, the parapolar, and the first few pairs of diapolar cells; parapolar cells short, seldom exceeding the calotte in length; uropolar cells usually verruciform, 1 to 3 additional verruciform cells sometimes present; axial cell ends anteriorly between the bases of the metapolar cells.

Vermiform larvae with abortive second axial cell just anterior to the end of the axial cell, between the basal ends of the metapolar cells, may attain length of 0.1 mm. or more before leaving the axial cell of the parent nematogen.

Rhombogens tend to be larger and broader than nematogens, with large, very prolific infusorigens; axial cell with same number of paranuclei as the number of infusorigens present; somatic cells of trunk in this phase with from 1 to 4 accessory nuclei.

Infusoriform 30 to 36 microns long, tapering to a conical point posteriorly, each cell in the urn with 2 nuclei and 1 germ cell.

Host.—*Octopus bimaculatus* Verrill and *O. bimaculoides* Pickford and McConnaughey.

Distribution.—Southern California.

Type specimens.—Syntypes on slide L-8, 2. Author's collection. Paratypes, other slides of the L-8 series.

This species resembles *D. californica* in size and cell number. It is distinguished by the fact that some or most of the somatic cells of the trunk are heavily charged with characteristic granules. Also it is generally broader, more robust-appearing, and the anterior diapolar cells play a more prominent part in the cephalic swelling, the calotte and parapolar cells a less prominent role.

Dicyemennea abelis n. sp.

(Pl. 1, figs. 8–10; pl. 2, figs. 24–27)

Diagnosis.—Adults 0.5 to 2.5 mm. long, usually not over 1.5 mm.; total number of somatic cells 23 to 29, most often 24 to 27; body slender, of about the same width throughout, transparent in life except for the parapolar, uropolar, and verruciform cells; diapolar cells of rhombogens sometimes heavily charged with granules; cephalic swelling comprised of the calotte, parapolar, and sometimes the first pair of diapolar cells, may sometimes be lacking, especially in rhombogens, owing to elongation and narrowing of the metapolar and parapolar cells; somatic cells of trunk tend to be arranged in opposed pairs but not rigidly so; axial cell ends anteriorly between the basal ends of the metapolar cells.

Vermiform larvae short and stocky, with sharply pointed calotte; the abortive second axial cell just anterior to the axial cell proper between the bases of the metapolar cells; larvae generally attaining a length of only 50 or 60 microns before their escape from the parent nematogen.

Rhombogens with accessory nuclei in some of the somatic cells of the trunk, the axial cell containing the same number of paranuclei as the number of infusorigens present; metapolar and parapolar cells tend to be elongated and narrowed so that there is no swelling at the anterior end.

Infusoriform 40 to 45 microns long, rounded posteriorly, each cell within the urn containing two free nuclei and one germ cell.

Chromosome number.—Diploid number estimated to be about 18 to 20.

Host.—*Octopus bimaculatus* Verrill.

Distribution.—Coast of southern and Lower California.

Type specimens.—Syntypes on slide 106-2. Author's collection. Paratypes, other slides of the 106 series.

This species resembles *D. californica* but is smaller, with fewer somatic cells, and the vermiform larvae are much smaller and stockier when fully developed within the parent nematogens. The tendency for the metapolar and parapolar cells to elongate at the beginning of the rhombogen phase is more pronounced in this species. The infusorigens are smaller and the number of embryos contained in a parent nematogen or rhombogen is more limited.

Dicyemennea adscita n. sp.

(Pl. 1, fig. 6; pl. 3, fig. 37)

Diagnosis.—Adults mostly 1 to 3 mm. long; total number of somatic cells 23, sometimes more; body slender, of about the same breadth throughout or slightly constricted for a short distance behind the cephalic swelling, transparent in life except the parapolar, uropolar, and verruciform cells; commonly 2 verruciform cells in addition to the uropolars, all verruciform cells characterized by the presence of many small, irregularly shaped, deeply staining granules scattered in the cytoplasm between the vacuoles; cephalic swelling moderate, composed of the calotte and parapolar cells; calotte orthotropal, short, generally wider than long, the propolar cells about one-third to one-half the diameter of the metapolars; metapolars only slightly longer than wide; parapolar cells about equal to the calotte in length, rounded posteriorly, adjoined by 1 dorsal and 1 ventral trunk cell; somatic cells of trunk, including the parapolars, arranged in 7 opposed pairs; axial cell ends anteriorly between the basal ends of the metapolar cells.

Rhombogens with only a few accessory somatic nuclei; the axial cell with the same number of paranuclei as the number of infusorigens present.

Infusoriform 33 to 36 microns long, bluntly pointed behind, each cell within the urn containing 2 free nuclei and 1 germ cell.

Chromosome number.—Diploid number estimated to be about 16.

Host.—*Octopus* sp.

Distribution.—Known only from an octopus dredged from a sand-and-mud bottom in about 35 fathoms of water off Point Loma, San Diego County, California. This octopus also contained *Dicyema balamuthi*. Five specimens of this species of *Octopus* were taken. They differed from *O. bimaculatus* in being of a lighter, more yellowish color, lacking the oculations at the bases of the third arms, and in the hectocotylus. The specimens were submitted to Dr. S. S. Berry of Redlands, who reports that they belong to an undescribed species. One of the five contained *Dicyemennea adscita* and *Dicyema balamuthi*. The other four contained *Dicyema balamuthi* and *Conocyema adminicula*.

D. adscita resembles *D. abelis*, from which it differs in slightly larger average size, lower and more constant cell count, generally shorter and broader calotte, and more prominent verruciform cells with characteristic dark-staining inclusions. The uropolar cells are not as constantly verruciform.

Dicyemennea abasi n. sp.

(Pl. 1, fig. 14; pl. 3, figs. 38–39)

Diagnosis.—Adult nematogens 0.3 to 0.9 mm. long; total number of somatic cells variable, from 22 to 26, different larvae in the same nematogen sometimes varying over most of the range; body generally widest in the anterior third of the trunk, tapering slightly posteriorly, or of nearly equal breadth throughout; no verruciform cells or heavy accumulations of granules; calotte orthotropal, conical, generally narrower than the anterior part of the trunk; propolar cells about one-third to one-half as large as the metapolars; axial cell ends anteriorly between the basal ends of the metapolar cells; vermiform larvae with rudimentary second axial cell between the bases of the metapolar cells. Rhombogen unknown.

Host.—*Octopus* sp., probably *bimaculoides* Pickford and McConnaughey.

Distribution.—Balboa Bay, Orange County, California.

Type specimens.—Syntypes on slide 103-14. Author's collection. This slide also contains *Dicyemennea abbreviata* and *Dicyema acciaccatum*. They are all very small species, but are so distinctive that there is no likelihood of confusing them.

Dicyemennea brevicephala McConnaughey, 1941

(Pl. 1, fig. 7; pl. 3, figs. 33–36)

Diagnosis.—Small dicyemids, adults usually not exceeding 1 mm. in length although occasional individuals may reach as much as 2 mm.; total number of somatic cells 27, rarely 26 or 28; body broad, of about equal breadth throughout; calotte flattened, discoid, capping the broad truncated ends of the large parapolar cells, often plagiotropal; propolar cells much smaller than the metapolar cells which surround them, the whole forming a flattened or convex disk with the propolars in the center, seldom exceeding the trunk in diameter, cilia of calotte shorter and denser than on the trunk; axial cell broad, extending to the propolar cells, ending bluntly anteriorly; somatic cells of trunk sometimes charged with refractile granules; verruciform cells 0 to 3, not prominent.

Rhombogens slightly larger than nematogens, with accessory nuclei in some of the trunk cells; axial cell with same number of paranuclei as the number of infusorigens present.

Infusoriform generally 35 to 40 microns long, rounded posteriorly, each cell within the urn containing 2 nuclei and 1 germ cell, the latter often elongated and pycnotic in appearance in mature infusoriforms. The refringent bodies are very large, occupying about one-half the body length. The granules elaborated by the capsule cells are large, attaining almost the size of the nuclei within the urn cells.

Chromosome number.—Diploid number estimated at about 18 or 20.

Host.—*Octopus apollyon* (Berry).

Distribution.—Marine View Rocks, San Mateo County; and Monterey Bay, California.

Dicyemennea abbreviata n. sp.

(Pl. 1, fig. 11; pl. 3, figs. 30–32)

Diagnosis.—Adults rarely exceeding 1 mm. in length; total number of somatic cells constant, 25; body short, stout, of about the same diameter throughout its length, truncated at the ends; calotte plus parapolar cells forming a cephalic swelling sometimes exceeding the width of the trunk and sharply set off from it by a strong constriction; metapolar and parapolar cells extend forward peripherally to or ahead of the small propolar cells, the whole complex forming a flattened or even concave disc with the 4 small propolar cells in the center, ringed by the 5 larger metapolar cells, these in turn by the crescentic parapolar cells; calotte proper set apart by markedly greater affinity for stains so that it forms a dark plaque contrasting with the rest of the body in stained preparations. Parapolar cells, though included in the cephalic swelling, stain more like other trunk cells; somatic cells of trunk, including the parapolars, arranged in 8 pairs, the caudal pair usually slightly inflated and verruciform.

Vermiform larvae with rudimentary second axial cell just anterior to the axial cell proper near the base of the propolar cells.

Rhombogens with indefinite number of accessory nuclei in some of the somatic cells of the trunk, the axial cell containing the same number of paranuclei as the number of infusorigens present, usually only 1 or 2.

Infusoriforms 37 to 41 microns in length, with 2 free nuclei and 1 germ cell in each of the cells within the urn; only a few infusoriforms present at any one time in a rhombogen, owing to the limited size of the vermiform individuals and the fact that the infusoriforms are not correspondingly reduced in size.

Chromosome number.—Diploid number estimated to be about 16 to 20.

Host.—*Octopus* sp., probably *bimaculoides* Pickford and McConnaughey.

Distribution.—Balboa Bay, Orange County, California.

Type specimens.—Syntypes on slide 103-14. Author's collection.

In size, cell number, and bodily characteristics this species is intermediate between *Dicyemennea brevicephala* and *Conocyema adminicula.*

Genus DICYEMA von Kölliker, 1849

Diagnosis.—Calotte 8-celled, 4 propolar and 4 metapolar cells, the 2 sets corresponding in position relative to the planes of symmetry of the calotte (except in D. truncatum), often plagiotropal in the adults; vermiform larvae without a small second axial cell.

Type species.—*Dicyema paradoxum* von Kölliker, 1849.

Synonym: *Dicyema clausianum* van Beneden, 1882.

KEY TO THE SPECIES OF DICYEMA[*]

1.	Somatic cells usually 22 or more	2
	Somatic cells less than 22	13
2. (1)	Medium-sized or small species, rarely exceeding 4.5 mm.	3
	Large species, commonly exceeding 5 mm.	12

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[*] Subsequent to the preparation of this manuscript and its submission for publication, an additional species of *Dicyema* was found on slides from an immature octopus from Lower California. This species was named *D. sullivani* and described by the writer in a separate article—McConnaughey (1949). At that time the distinction between *Octopus bimaculatus* and *O. bimaculoides* had not been made. It is reasonably certain that the host is *O. bimaculoides*, not *O. bimaculatus* as given. See Pickford and McConnaughey (1949).

3. (2) Axial cell extends forward to the propolar cells.......................... 5

Axial cell ends anteriorly at the base of or between the bases of the metapolar cells, not extending forward to the propolars.......................... 4

4. (3) Calotte acutely pointed, propolar cells much smaller than the metapolars; nuclei with large irregular masses of chromatin.......................*acheroni* n. sp.

Calotte not sharply pointed; propolar cells about half as large as the metapolars; nuclei with rounded nucleolus and only small peripheral granules of chromatin ....*acciaccatum* n. sp.

5. (3) Width of calotte aproximately the same as or less than that of the anterior end of the trunk 6

Width of calotte exceeds that of the anterior end of the trunk, from which it is well marked off 12

6. (5) Somatic cells characteristically 26, vary from 25 to 27.

> A robust, medium-sized species up to 2.5 mm. long, commonly with from 1 to 6 verruciform cells; calotte hemispherical, orthotropal, not usually exceeding trunk in width. Hosts: *Octopus de filippi* Vérany and *Sepiola steenstrupiana* Lévy. Distribution: Mediterranean..................*microcephalum* Whitman, 1883

Somatic cells characteristically 22.......................... 7

7. (6) Calotte globular or elongate, seldom discoid, generally as long as or longer than broad 8

Calotte usually flattened, somewhat discoid, wider than long; short stocky species 9

8. (7) Infusoriform with 2 nuclei and 1 germ cell in each cell within the urn; axial cell of vermiform individuals often swollen anteriorly within the calotte, especially in rhombogens..........................*apollyoni* Nouvel, 1947

Infusoriform with 1 nucleus and 1 germ cell in each cell within the urn; axial cell of vermiform phases narrows rather than broadens within the calotte.

> Small, generally under 1 mm. Hosts: *Octopus vulgaris* and *Octopus fangsiao*. Distribution: near Misaki, Japan.........*misakiense* Nouvel and Nakao, 1938

9. (7) Anterior ends of parapolar cells completely encircle axial cell................10

Anterior ends of parapolar cells do not completely encircle axial cell; first 2 diapolars extend forward between parapolars to base of metapolar cells.

> Short stocky species, generally 0.5–1.5 mm. long; no distinct cephalic swelling; calotte of adults much wider than long, with very short metapolar and parapolar cells. Hosts: *Rondeletiola minor* Naef and *Sepietta oweniana* (d'Orb.). Distribution: Mediterranean......................*rondeletiolae* Nouvel, 1947

10. (9) Metapolar cells regularly alternate with propolars in position relative to planes of symmetry of calotte; uropolar cells commonly verruciform.

> Short stocky species with small discoid calotte. Hosts: *Sepia officinalis* Linnaeus, *Sepia orbignyana* Férussac, *Sepia esculenta* Hoyle and *Rossia macrosoma* (Della Chaije). Distribution: Mediterranean and Atlantic coasts of Europe; Japan ....*truncatum* Whitman, 1883

Metapolar cells correspond with propolars in position relative to planes of symmetry of calotte, or at least do not regularly and constantly alternate with them; uropolar cells not verruciform..........................11

11. (10) Adults 0.5 to 1.0 mm. long; calotte discoid, small, telescoped; parapolar cells very short, not pointed behind; first diapolar cells make up most of the cephalic swelling; no true verruciform cells.

> Hosts: *Sepia elegans* d'Orb. and *Rondeletiola minor* Naef. Distribution: Mediterranean..........................*schulzianum* van Beneden, 1876

Adults 1.5 to 3.6 mm. long; calotte nearly hemispherical in young, often flattened and much wider than long in adults; nuclei with large eosinophilic nucleoli.

> Hosts: *Sepioteuthis lessoniana* Férussac. Distribution: Japan ....*orientale* Nouvel and Nakao, 1938

12. (5) Calotte short, hemispherical, usually broader than long, forming well-marked cephalic swelling; propolar cells about same size as or even larger than metapolars; commonly with 1 to 5 verruciform cells; somatic cells 25 to 28.

> Length: 2 to 3 mm. Hosts: *Octopus macropus* Risso and *O. vulgaris* Lamarck. Distribution: Mediterranean and Atlantic coasts of Europe, and Mauritania, French West Africa..........................*paradoxum* von Kölliker, 1849
> (Synonym: *clausianum* van Beneden, 1882)

Calotte elongate, propolar cells usually smaller than metapolars; no verruciform cells; somatic cells 22..*balamuthi* n. sp.

13. (2) Calotte usually flattened and oblique, with rounded or quadrilobate face exceeding diameter of trunk, free edges of metapolar cells extending out as platelike margin; somatic cells 28 to 33, usually 30 or 31.

Large, sometimes up to 7 mm., relatively thin; 0 to 5 verruciform cells. Hosts: *Sepietta oweniana* (d'Orb.), *Sepietta obscura* Naef, *Sepiola steenstrupiana* Lévy, and *Sepia elegans* d'Orb. Distribution: Mediterranean ....*macrocephalum* (van Beneden, 1878)

Calotte variable but not flattened or platelike; somatic cells typically 24, varying from 22 to 26.

Long slender species often 5 to 6 mm.; commonly with 1 or 2 large verruciform cells. Hosts: *Eledone moschata* (Lamarck) and *Sepiola rondeleti* Steenstrup. Distribution: Mediterranean.....................*moschatum* Whitman, 1883

14. (1) Axial cell extends to base of propolar cells..............................15

Axial cell does not reach propolar cells..................................16

15. (14) Somatic cells usually 18 or 19.

Stocky; calotte usually not exceeding anterior end of trunk in width; metapolars widest posteriorly. Hosts: *Octopus vulgaris* Lamarck. Distribution: Mediterranean, Atlantic coast of Europe, North Sea..........*typus* van Beneden, 1876

Somatic cells 16 or less.

Small, thin; cephalic swelling (calotte plus parapolars) conspicuously wider than, and well marked off from, the thin trunk; metapolar cells often widest anteriorly. Hosts: *Octopus* sp. (either *vulgaris* or *rugosus*). Distribution: Mauritania, French West Africa...............*megalocephalum* Nouvel, 1934

16. (14) Somatic cells 18 or 19; axial cell bluntly rounded anteriorly ending near the posterior ends of the metapolar cells; calotte conical, tapering to bluntly rounded point.

Small, massive, less than 1 mm. long. Hosts: *Octopus vulgaris* Lamarck. Distribution: Japan.................................*acuticephalum* Nouvel, 1947

Somatic cells usually 16 or less; axial cell pointed anteriorly and insinuated farther forward between the metapolars but not reaching the propolars.

Small, massive, seldom exceeding 0.5 mm.; cilia of calotte markedly shorter and more close set than on trunk. Host: *Octopus* sp. (*vulgaris* or *rugosus*). Distribution: Mauritania, French West Africa..................*monodi* Nouvel, 1934

Dicyema apollyoni Nouvel, 1947

(Pl. 4, fig. 48; pl. 5, figs. 51–55)

Diagnosis.—Adults 0.5 to 3.0 mm. long; total number of somatic cells 22; rhombogens usually broader and longer than nematogens; body broad, robust-appearing, transparent, not heavily granular, of nearly the same breadth throughout, or slightly wider at the anterior end; calotte orthotropal, broadly rounded or squarish, of about the same diameter as or somewhat exceeding the trunk; cephalic swelling composed of calotte, parapolar, and first pair of diapolar cells, often not well marked; propolar cells usually about equal in size to metapolars, sometimes exceeding them; parapolar cells subequal to calotte, shield-shaped, pointed behind; axial cell penetrates forward between bases of propolar cells, rounded or even inflated at anterior end, calotte fitting over it in manner of helmet; trunk cells disposed in opposed pairs but this arrangement often obscured in adults; rhombogens with variable number of accessory nuclei in some somatic cells of trunk; paranuclei of axial cell correspond in number with the number of infusorigens present, usually 1 or 2.

Infusoriforms 27 to 35 microns long, slightly tapered and conical behind, each refringent body about the same size as, or slightly larger than, the urn; each cell within the urn with 2 nuclei and 1 germ cell.

Chromosome number.—Diploid number probably 14.

Host.—*Octopus apollyon* (Berry).

Distribution.—Marine View Rocks, San Mateo County, California, and Monterey Bay, California.

Dicyema balamuthi n. sp.

(Pl. 4, figs. 46–47; pl. 5, figs. 56–64; pl. 6, figs. 71–79)

Diagnosis.—Adults generally 0.75 to 2.5 mm. long, largest measured specimen 4.0 mm.; total number of somatic cells 22; body thin, transparent, of about uniform diameter throughout except for the enlarged calotte, without verruciform cells; cephalic swelling composed almost entirely of the calotte; parapolar cells only slightly thickened at junction with calotte, often noticeably unequal; calotte elongate, well marked off from, and broader than, the trunk; propolar cells commonly about two-thirds to three-fourths as long as metapolars; somatic cells of trunk, including the parapolars, disposed in 7 opposed pairs; axial cell penetrates calotte to, or between bases of, the propolar cells, its anterior end inflated in mature individuals.

Hosts.—*Octopus* sp. First found in a small octopus by Dr. William Balamuth in the San Francisco Bay area, the octopus not preserved, probably a small *O. apollyon* (Berry). Subsequently found in five specimens of an unidentified species of octopus dredged from about 35 fathoms off Point Loma in San Diego County, California. These octopuses have already been discussed in connection with the description of *Dicyemennea adscita.* A small red octopus dredged off Point Loma also contained numerous stem nematogens and young primary nematogens which have been tentatively assigned to this species.

Type specimens.—Syntypes on slide L-2, 6. Author's collection. Paratypes on other slides of the L-2 series. *Conocyema adminicula* is also present on these slides.

The axial nucleus in this species sometimes gives rise to additional free nuclei in the axial cell, through amitotic division, even in very young individuals, so that the number of free nuclei present in the axial cell of rhombogens may exceed the number expected from the number of infusorigens present, and they may also be encountered in the other phases before the formation of any infusorigens. The formation of nucleus-like bodies, other than paranuclei, from axoblasts during the period of transition of phase has also been noted.

The stem nematogen is typical of those of the genus *Dicyema*, having three axial cells in linear series, the anterior one lagging slightly behind the other two in its development. The calotte is somewhat flattened in the adult, the four metapolar cells alternating with the propolar cells. The total number of somatic cells in the clearest examples seen was 26. Old individuals may reach a length slightly exceeding 2 mm.

The vermiform larvae contained in the axial cells of mature stem nematogens are typical of those of the primary nematogens of this species.

Dicyema acciaccatum n. sp.

(Pl. 4, fig. 49; pl. 5, figs. 65–67)

Diagnosis.—Small dicyemids seldom reaching 1 mm. in length, the majority of mature individuals less than one-half mm. long; characteristic number of somatic cells 22 but occasional higher counts up to 28 observed; body stocky, of nearly the same breadth throughout, or sometimes broadest a short distance back of the calotte, tapering slightly towards both ends; axial cell ends anteriorly at the base of the metapolar cells; calotte elongate, not exceeding the trunk in diameter; propolar cells noticeably smaller than the metapolars; parapolar cells about equal to the calotte in length, adjoined posteriorly by 1 dorsal and 1 ventral trunk cell; cells of the trunk disposed as a rule in opposed pairs; no verruciform cells; the tendency to produce accessory nuclei at the beginning of the rhombogen phase is pronounced, starting early and producing more accessory nuclei than in most species; the paranuclei and also the axial nucleus may divide amitotically so that the number of free nuclei in the axial cell often considerably exceeds that expected from the number of infusorigens present; usually only 1 or 2 infusorigens; infusoriform 25 to 37 microns in length, rounded posteriorly, each cell within the urn containing 2 nuclei and 1 germ cell, the germ cell lightly staining except for 2 or 3 large deeply staining blocks of chromatin.

Host.—*Octopus* sp., probably *bimaculoides* Pickford and McConnaughey.

Distribution.—Balboa Bay, Orange County, California.

Type specimens.—Syntypes on slide 103-14. Author's collection.

This species differs from the majority of its congeners in that the axial cell terminates near the base of the metapolar cells rather than extending forward to the propolars. It differs from *D. monodi* and *D. acheroni* in size, proportions, cell number, cytological aspect of the nuclei, and other details; from *D. megalocephalum* in cell number and in the shape of the body and calotte.

Dicyema acheroni n. sp.

(Pl. 4, fig. 50; pl. 5, figs. 68–70)

Diagnosis.—Small to medium-sized dicyemids, adults mostly 0.5 to 1.5 mm. long; body slender, of approximately the same breadth throughout or slightly broader near the anterior end of the trunk; calotte orthotropal pointed, slightly longer than broad, not exceeding the anterior end of the trunk in breadth; propolar cells markedly smaller than the metapolars; axial cell ends bluntly at the posterior end of the metapolar cells, not extending forward to the propolars; trunk cells not conspicuously charged with granules and none of those examined showed verruciform cells; all nuclei with coarse irregular pieces and strands of chromatin peripherally, very different from the usual rounded nucleolus and small chromatin granules of most species; somatic cells vary in number from about 23 to 28.

The infusoriforms seem to have unusually elongated bodies but they were partly obscured by precipitation of stain around the refringent bodies and no precise details could be made out.

Host.—*Octopus* sp., probably *bimaculoides* Pickford and McConnaughey.

Distribution.—Balboa Bay, Orange County, California.

Type specimens.—Syntypes, slide 113-9. Author's collection.

The ending of the axial cell behind the metapolar cells separates this species from all others except *D. monodi, D. acciaccatum,* and *D. acuticephalum,* from which it differs in cell number, aspect of the nuclei, shape of the calotte, and proportions.

Genus CONOCYEMA van Beneden, 1882

Synonym: *Microcyema* van Beneden 1882

Diagnosis.—Dicyemids in which the axial cell of the adult is branched or irregular in shape. The somatic cells of some species may lose their cilia and fuse into a sort of syncytium in which individual cell boundaries cannot be distinguished. The known species are all small, with a constant number and arrangement of cells in the larvae.

The larvae are short, robust, usually with a strong constriction dividing the body into an anterior region composed of the calotte plus the parapolar cells, and a posterior region composed of the axial cell and the cells of the trunk enveloping it. The cells of the calotte stain more intensely than the others and may bear a prominent tuft of cilia directed forward. The remaining somatic cells bear cilia directed laterally or posteriorly. The total number of somatic cells in the species now known is smaller than in most ordinary dicyemids.

The infusorigens and infusoriforms are typical of those of dicyemids generally, showing no special distinguishing characteristics.

As here treated, this genus includes all the so-called heterocyemids. Since only three species are known, and these incompletely, it has seemed best to group them into one genus in view of the larval and adult characteristics which they have in common, rather than to follow previous authors in recognizing a separate genus for each species. If more species are discovered in the future and their relationships more clearly worked out, a sound basis for generic divisions may become apparent. In the present paper the generic name of the first described species is recognized as the proper generic name for the group.

Type species.—Conocyema polymorpha van Beneden, 1882.

KEY TO THE SPECIES OF CONOCYEMA

1. Somatic cells 10, only 2 of them posterior to the postcephalic constriction in the larvae. Adult very irregular and variable in shape, without cilia and with somatic cells fused into a syncytium in which cell boundaries are difficult or impossible to make out.
   Host: *Sepia officinalis* L. Distribution: Mediterranean and Atlantic coasts of Europe....................................*vespa* van Beneden, 1882
   Somatic cells more than 10 in number, more than 2 of them posterior to the postcephalic constriction in the larva....................................2
2. Somatic cells 12 (possibly 16), 4 large inflated anterior cells followed by 8 trunk cells. Adults irregular in shape, without cilia.
   Host: *Octopus vulgaris* Lamarck. *Distribution:* Mediterranean ....*polymorpha* van Beneden, 1882
   Somatic cells 17, cephalic swelling of 11 cells, followed by filiform trunk with 6 somatic cells ....*adminicula* n. sp.

Conocyema adminicula n. sp.

(Pl. 1, fig. 15; pl. 3, figs. 40–45)

Diagnosis.—Small dicyemids mostly not exceeding 1 mm. in length; total number of somatic cells 17; adult nematogens of striking appearance, the trunk slender and filiform as in typical dicyemids, the anterior end, comprising the calotte plus the parapolar cells, greatly inflated, giving the organism as a whole the appearance of a flower on a stalk; metapolar cells especially inflated, each invaded by a branch from the anterior end of the axial cell; in old nematogens the portion of the axial cell contained in the swollen calotte may exceed that in the trunk and contain the axial nucleus together with most or all of the germ cells and developing embryos; metapolar and parapolar cells vacuolated and sometimes with large round eosinophilic bodies, presumably material derived from host tissue cells in the course of digestion, attached to the surface and inside the cells in vacuoles.

Vermiform larvae short, robust-appearing, without any abortive second axial cell; a noticeable constriction at the base of the parapolar cells; calotte staining more intensely than the remainder of the body, forming a dark plaque at the anterior end; body of the larva entirely ciliated, those on the calotte prominent and directed forward; cephalic swelling comprised of 11 cells, 4 propolars, 5 metapolars, and 2 parapolars; the remainder of the body forming the trunk composed of the axial cell and 6 enveloping somatic cells; the number and arrangement of cells very constant.

Hosts.—At least two, possibly three, species of unidentified *Octopus* dredged off Point Loma, San Diego County, California, and from near the Coronado Islands. The octopuses have been submitted to Dr. S. S. Berry of Redlands.

Type specimens.—Syntypes, slides of the L-11 series. Author's collection.

This species is intermediate in structure between the typical dicyemids of the genus *Dicyemennea* and the heterocyemids previously known, exhibiting both the filiform trunk characteristic of the former, together with the branching irregular shape of the axial cell, anteriorly at least, and the larval characteristics of the latter. It appears to be most closely related to *Dicyemennea abbreviata* which may illustrate the first definite step toward the heterocyemid condition.

THE STATUS OF THE FAMILY CONOCYEMIDAE*

Gersch (1938) maintained that the forms described by van Beneden (1882), and subsequently observed by Lameere (1916, 1918, 1919) and Nouvel (1936, 1937) as "heterocyemids," actually represent stages in the degeneration of old individuals of ordinary dicyemids or misinterpretation of damaged or poorly fixed specimens. He claimed to have found all intermediate conditions between the true dicyemids and the heterocyemids among degenerating individuals of *Dicyema typus* and *Dicyemennea eledones.*

Hartmann (1939) briefly reviewed this question and pointed out that, while Gersch's illustrations do correctly represent degenerating individuals of ordinary dicyemids, they do not at all represent the heterocyemids. The distinctive characters of the young larvae, for one thing, were entirely ignored by Gersch, as well as the question of relative sizes. From his study of the literature and the fact that he too on one occasion had found heterocyemids, Hartmann concluded that Gersch was entirely mistaken on this question.

Schartau (1940) published a study of heterocyemids found by him at Naples and concluded that the heterocyemids are good species and the family a valid one.

Nouvel (1947) has summarized the findings of all previous authors with regard to the heterocyemids and treats them as a valid family.

My own study of the question, together with the fact that I have found heterocyemids showing clearly all ages from young vermiform embryos to adult nematogens and young rhombogens, enables me to confirm the views of Hartmann, Schartau, Lameere, and Nouvel on this question. There can be no doubt that the organisms described as heterocyemids are species in their own right and not degenerating individuals of other dicyemids.

It is uncertain whether they constitute a natural group, or simply represent an extreme condition, characterized by reduction of the trunk and expansion of the axial cell into the greatly inflated cephalic swelling, which condition may have arisen independently from the two common genera.

Conocyema adminicula seems clearly related to the genus *Dicyemennea.* A series of species can be selected showing transitional characteristics in small steps from typical *Dicyemennea* such as *D. californica* to the heterocyemid *C. adminicula.* All are alike in having a calotte of 4 propolar cells and 5 metapolar cells and an elongated trunk. The series could be selected as follows:

Dicyemennea californica: Medium to large size; large, variable number of somatic cells (30 to 38); axial cell terminating anteriorly at the base of the metapolar cells; vermiform larvae with an abortive second axial cell anterior to the definitive axial cell near the back of the metapolar cells; calotte not markedly different in staining characteristics from the trunk.

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* The name Heterocyemidae was given to these organisms by van Beneden (1882), and has been used by most subsequent investigators. Stunkard (1937) pointed out that this name was not a valid family name since there is no genus *Heterocyema.* He proposed the name Conocyemidae in its place.

Since these species have been termed heterocyemids by almost all writers on the subject and this has become the familiar name for the group, its use is continued here for convenience.

Dicyemennea abelis: Similar to the foregoing but smaller and with a lower cell count.

Dicyemennea brevicephala: Smaller size; greater cell constancy, cell number nearly always 27; axial cell extends forward to the base of the propolar cells; abortive second axial cell of larvae well forward next to the propolar cells; calotte of adult flattened, disklike.

Dicyemennea abbreviata: Very small size; cell number rigidly constant, 25; calotte flat or even concave, deeply staining as compared to the trunk, its cilia directed forward; a prominent groove separating the cephalic swelling (calotte plus parapolar cells) from the trunk; abortive second axial cell of vermiform larvae well forward against the propolar cells.

Conocyema adminicula: Very small size; cell number rigidly constant, 17; no abortive second axial cell in the vermiform larva; separation of cephalic swelling from the rest of the trunk even more marked; axial cell branching into the much swollen metapolar cells in the adult, becoming very irregular in older individuals; filiform trunk retained.

Conocyema vespa might be thought of as continuing this series further, with still greater reduction of the trunk to two somatic cells and of the calotte to six. It is not clear to what other dicyemids it is most closely related.

Conocyema polymorpha is not described with enough definiteness to place it in this series with certainty. If the four large granular lobes at the anterior end represent metapolar cells rather than propolars, it might be considered to stand in much the same relation to *Dicyema* as *Conocyema adminicula* does to *Dicyemennea.*

Further study of *Conocyema polymorpha* and the description of additional species showing the heterocyemid condition are necessary before it can be decided whether the heterocyemids constitute a natural group or whether they arose in a polyphyletic manner as extreme forms from both the other genera.

The distinctive larval and adult characteristics of the heterocyemids are such as to make it convenient to group them together as a unit at present. Until the group is better known, there seems no good reason for recognizing separate genera for the three species. The writer agrees with Lameere that they are not sufficiently different from other dicyemids to warrant placing them in a separate family.

Genus Dicyemodeca Wheeler, 1897

(Pl. 7, figs. 80–89)

Wheeler (1897) named this genus for dicyemids found by him in the region of San Diego Bay, California, which differed from other known dicyemids in the possession of 10 cells in the calotte, the 4 propolar cells being followed by 6 instead of the usual 4 or 5 metapolar cells. He recognized one species for which he proposed the name *Dicyemodeca sceptrum.* Other students of the group have never reported such forms.

While restudying the dicyemids from the San Diego Bay region, the writer has confirmed Wheeler's observation that forms with 10 cells in their calotte do occur. However, their occurrence, so far as my observations go, is very rare and irregular—single individuals or only a few being found on slides containing many ordinary dicyemids with which they seem in other respects conspecific. Thus "deca" individuals have been found on slides of *Dicyemennea californica, Dicyemennea granularis, Dicyemennea abelis,* and a single such specimen of *Conocyema adminicula.* All the abnormal specimens appeared otherwise conspecific with the predominant species on the slides. Furthermore, one large nematogen showing this condition contained several well-developed vermiform larvae all of which were normal and typical of *Dicyemennea californica.*

Twice, individuals of *D. californica* with 5 propolar cells were found, which thus arrived at a "deca" condition by a different means, and one of *D. granularis* in which both the propolar and metapolar groups of cells were increased by one, giving the calotte 11 cells.

It appears then that the genus *Dicyemodeca* must be regarded as founded upon aberrant individuals and cannot be recognized as a valid taxonomic category. Should this malformity prove hereditary and become established so that distinct and separate populations of *Dicyemodeca* occur, they might perhaps deserve recognition with as much justification as do the genera now recognized.

In the spontaneous appearance of this character in four different species there is seen the possibility of the polyphyletic origin of one or more of the genera now recognized.

NOTE ON THE OCTOPUS BIMACULATUS COMPLEX OF SOUTHERN CALIFRONIA

The cephalopods along the coast of southern California, which have been known as *Octopus bimaculatus* Verrill, actually represent two species differing most conspicuously in the size of the eggs and of the adults. In former publications on West Coast cephalopods, and on their parasites, Verrill's name was used for both forms. The smaller, large-egged octopus has been named *Octopus bimaculoides* Pickford and McConnaughey, 1949. Verrill's name is the valid one for the larger, small-egged form.

Unfortunately the octopuses from Balboa Bay, California, from which some of my earlier collections of mesozoa were made, were not preserved, so it is impossible to state with certainty to which species they belonged. Also no sure way has been found to determine to which species very young octopuses belong.

Some of the early Balboa Bay collections contained species of mesozoa not subsequently encountered (*Dicyemennea abasi, Dicyemennea abbreviata, Dicyema acciaccatum* and *Dicyema acheroni*). Since these octopuses were taken in a shallow mud flat area at Balboa Bay it seems probable that they were *O. bimaculoides.*

Wheeler (1897, 1899) studied the dicyemids of "*Octopus punctatus*" from the San Diego Bay region, California, and reported the presence of three species, which he named *Dicyema coluber, Dicyemennea whitmanii,* and *Dicyemodeca sceptrum.* It appears probable that the octopuses studied by

Wheeler comprised both species that have been confused under the name *O. bimaculatus* Verrill, and possibly a third species. He published no illustrations or descriptions of the dicyemids he named that are sufficient to permit definite identification. The genus *Dicyemodeca* appears to have been based on aberrant individuals of certain species of *Dicyemennea*. The specific names proposed by Wheeler are considered to be *nomina nuda*.

SUMMARY

Cephalopods of the Pacific coast in a section from San Francisco Bay to Rosarito Beach, Lower California, and including the Coronado Islands, have been examined for dicyemids. A small series of octopuses from the Hawaiian and Marshall islands were also examined, but were found not to be infected.

Twelve species of dicyemids, all distinct from those reported from Europe and Japan, were found. Descriptions and illustrations of these are presented. Nine of them are new species.

The existence of the heterocyemid group, denied by Gersch, is confirmed. The genus *Conocyema* is revised to include all of the three species now known.

The existence of the stem nematogen, denied by Gersch, is confirmed. The stem nematogen of *Dicyema balamuthi* is described.

Evidence is presented to show that the genus *Dicyemodeca* was founded on aberrant individuals and is not a valid taxonomic category.

There are two species of *Octopus*, common along the coast of southern California, which have been confused under the name *Octopus bimaculatus* Verrill.

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PLATES

PLATE 1

The known species of genus *Dicyemennea* and *Conocyema* all drawn to the same scale to show general characteristics of size and proportions. All figures except 3, 4, 5, 16, and 17 made with the aid of a camera lucida from preparations in the author's collection.

Fig. 1. *Dicyemennea californica.*

Fig. 2. *Dicyemennea granularis.*

Fig. 3. *Dicyemennea eledones* (based on description by Whitman).

Fig. 4. *Dicyemennea lameerei* (based on description by Nouvel).

Fig. 5. *Dicyemennea gracile* (based on description by Whitman).

Fig. 6. *Dicyemennea adscita.*

Fig. 7. *Dicyemennea brevicephala,* five normal and one giant individual.

Figs. 8 to 10. Groups of *Dicyemennea abelis* taken from different individual octopuses, showing variation in size.

Fig. 11. *Dicyemennea abbreviata.*

Fig. 12. *Dicyemennea californica,* abnormal individual with six metapolar cells (see pl. 7 for details).

Fig. 13. *Dicyemennea californica,* another abnormal individual with six metapolar cells.

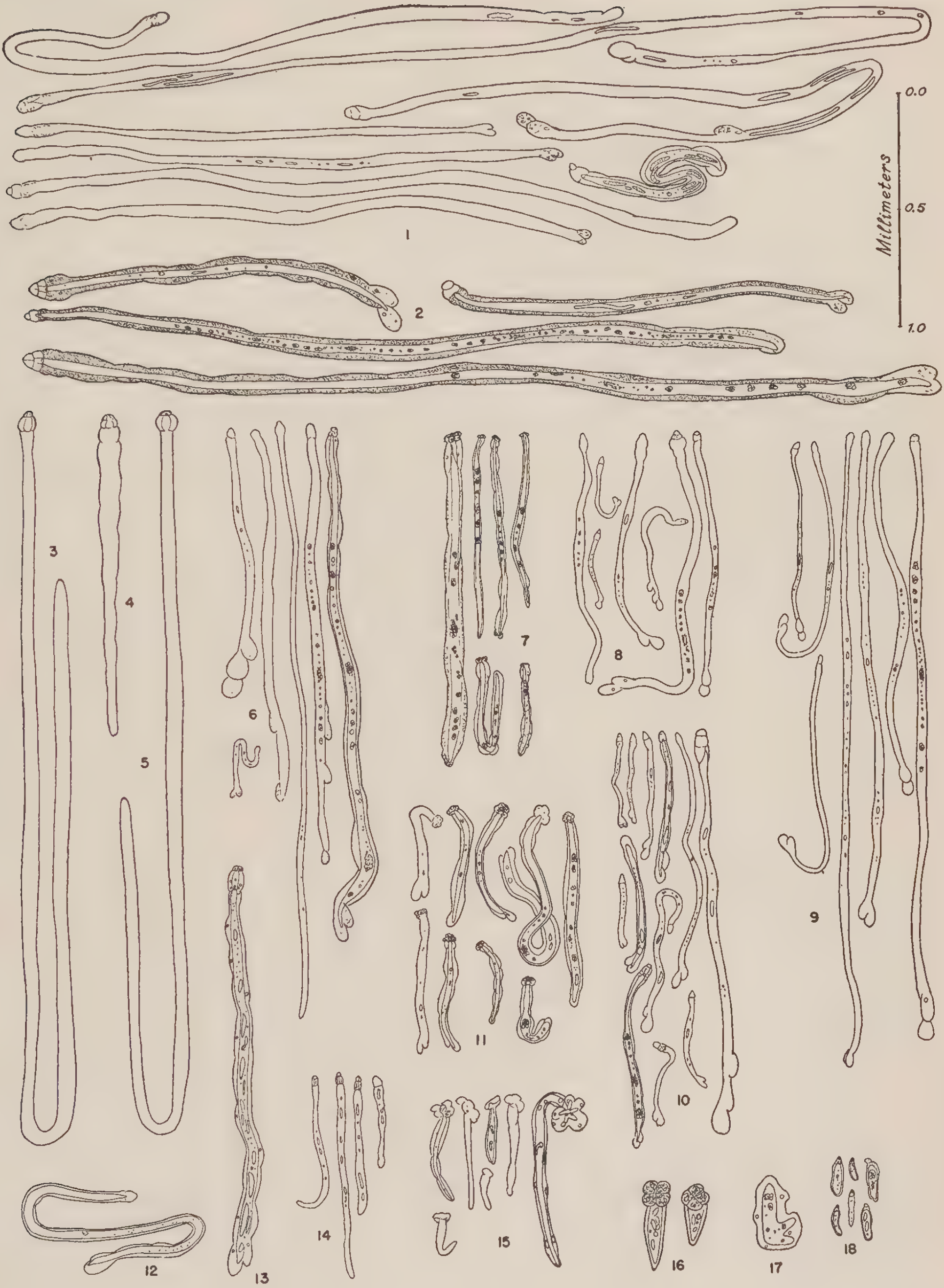
Fig. 14. *Dicyemennea abasi.*

Fig. 15. *Conocyema adminicula.*

Fig. 16. *Conocyema polymorpha* (from description by van Beneden).

Fig. 17. *Conocyema vespa* (from description by Lameere).

Fig. 18. Small unnamed species of *Dicyemennea* for which there has not yet been sufficient material on hand from which to draw up a satisfactory description. From *Octopus bimaculatus* Verrill, Balboa Bay, California.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Millimeters
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PLATE 2

Fig. 19. *Dicyemennea californica,* young nematogen (scale A).

Fig. 20. *Dicyemennea californica,* anterior end of an individual transitional between the nematogen and rhombogen phases, some fusiform axoblasts in the axial cell (scale A).

Fig. 21. *Dicyemennea californica,* anterior end of a large nematogen (scale A).

Fig. 22. *Dicyemennea californica,* vermiform larva inclosed in the axial cell of a nematogen (scale C).

Fig. 23. *Dicyemennea abelis,* vermiform larva inclosed in the axial cell of a nematogen (scale C).

Fig. 24. *Dicyemennea abelis,* young primary rhombogen showing binucleate axoblasts at either end of the row of axoblasts (scale B).

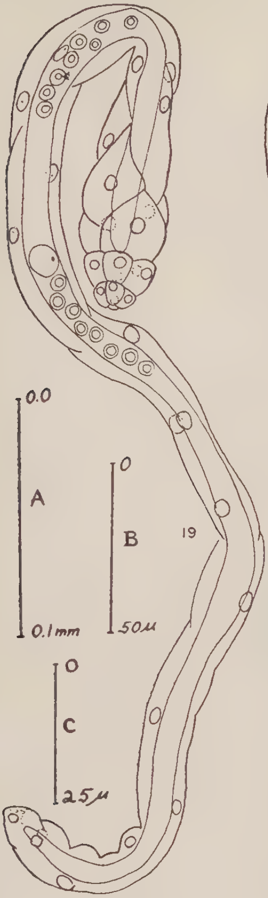
Fig. 25. *Dicyemennea abelis,* anterior end of a nematogen (scale A).

Fig. 26. *Dicyemennea abelis,* anterior end of a young rhombogen showing elongation of the metapolar and parapolar cells (scale A).

Fig. 27. *Dicyemennea abelis,* broad form of young vermiform individual shortly after escape from the axial cell of the parent nematogen (scale C).

Fig. 28. *Dicyemennea granularis,* anterior end of a rhombogen (scale A).

Fig. 29. *Dicyemennea granularis,* anterior end of a rhombogen (scale A).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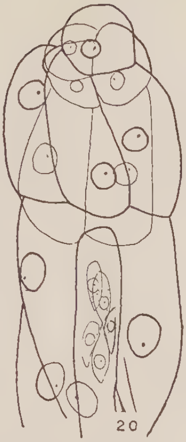

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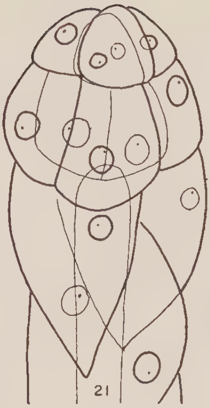

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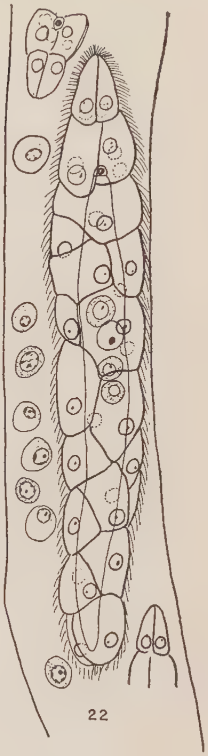

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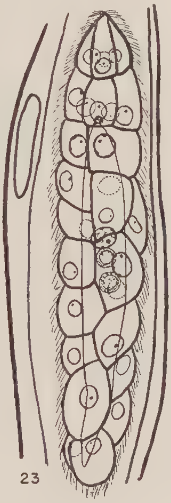

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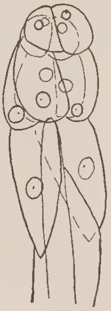

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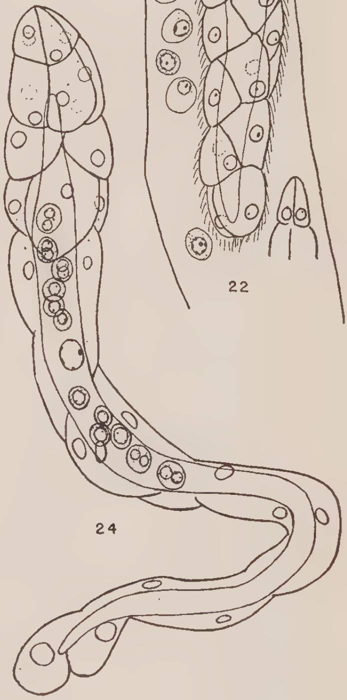

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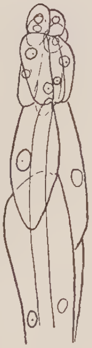

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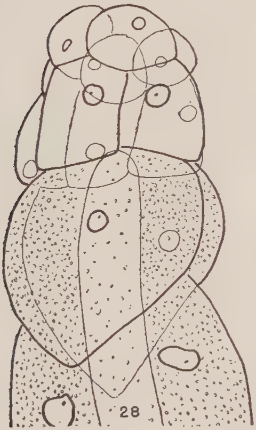

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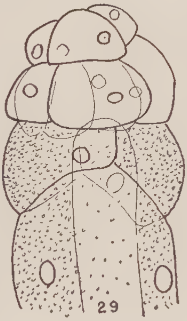

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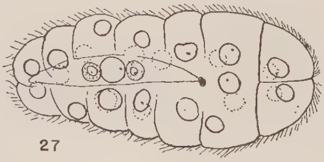

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PLATE 3

Fig. 30. *Dicyemennea abbreviata,* nematogen (scale A).

Fig. 31. *Dicyemennea abbreviata,* calotte and parapolar cells in polar view showing the disposition of the cells (scale B).

Fig. 32. *Dicyemennea abbreviata,* optical frontal section of a young vermiform larva showing the small abortive second axial cell anterior to the axial cell proper, and the characteristic position of the axial cell nucleus in front of both of the first two axoblasts (scale D).

Fig. 33. *Dicyemennea brevicephala,* anterior end of a rhombogen (scale B).

Fig. 34. *Dicyemennea brevicephala,* anterior end of a young rhombogen with the calotte oblique showing the disposition of the cells (scale B).

Fig. 35. *Dicyemennea brevicephala,* anterior end of a young rhombogen (scale B).

Fig. 36. *Dicyemennea brevicephala,* vermiform larva within the axial cell of a nematogen; the pycnotic remnant of the abortive second axial cell in late stage of degradation in one of the propolar cells (scale D).

Fig. 37. *Dicyemennea adscita,* anterior end of a rhombogen (scale A).

Fig. 38. *Dicyemennea abasi,* anterior end of a nematogen (scale B).

Fig. 39. *Dicyemennea abasi,* anterior end of another nematogen (scale B).

Fig. 40. *Conocyema adminicula,* anterior end of a young nematogen, showing the branching of the axial cell into the metapolar cells (scale B).

Fig. 41. *Conocyema adminicula,* anterior end of a young nematogen (scale D).

Fig. 42. *Conocyema adminicula,* very young individual shortly after its escape from the parent nematogen (scale D).

Fig. 43. *Conocyema adminicula,* young individual with the axial cell just beginning to branch into the metapolar cells; polar view of the cephalic swelling to show the disposition of the cells (scale D).

Fig. 44. Optical section of the calotte of the same individual as in fig. 43, showing the branching of the axial cell into the metapolar cells (scale D).

Fig. 45. Optical section at the level of the parapolar cells to show the narrowing of the axial cell as it passes from the inflated calotte to the trunk.

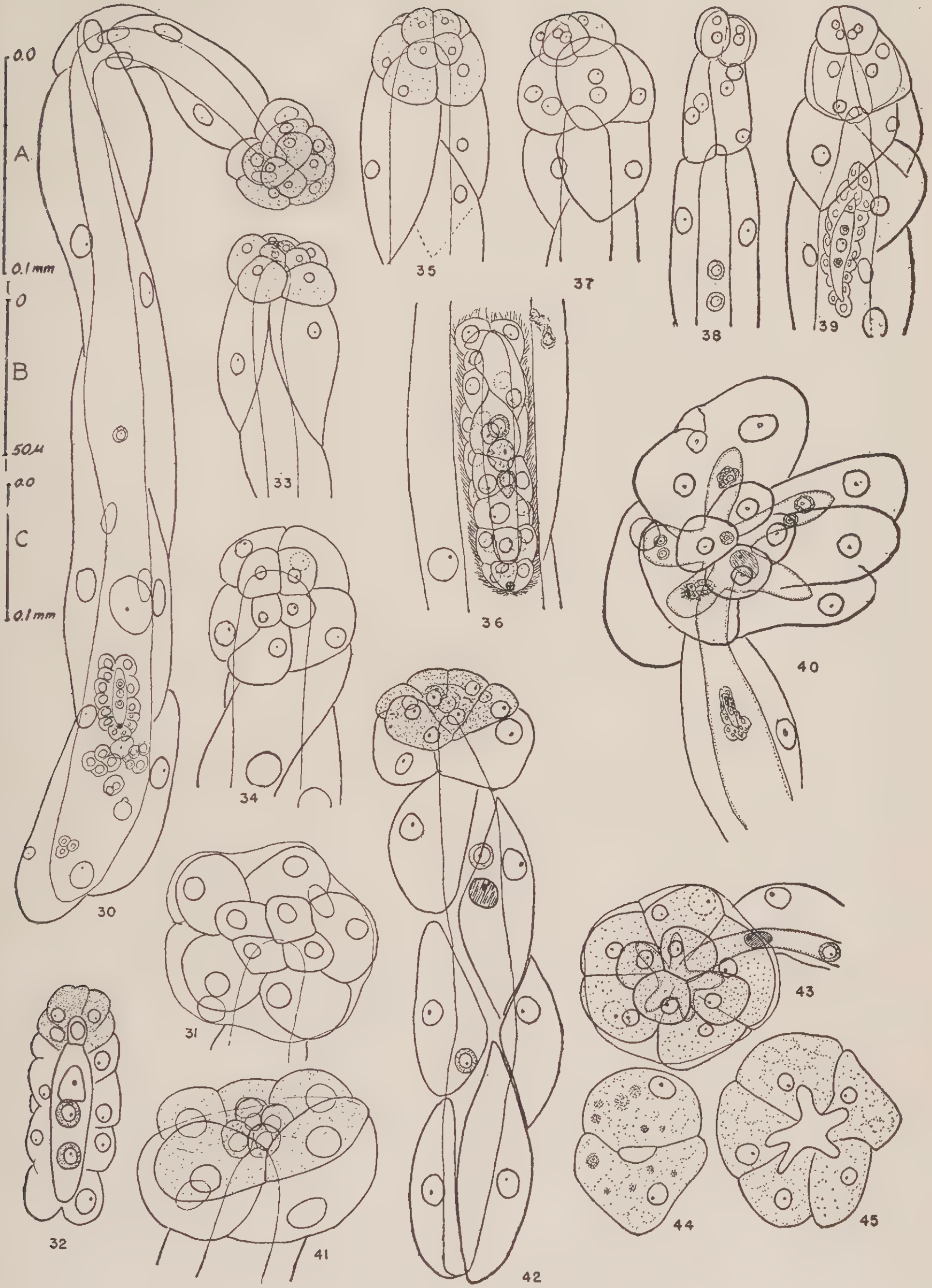
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PLATE 4

The species of *Dicyema* from California, all drawn to the same scale to show general characteristics of size and form.

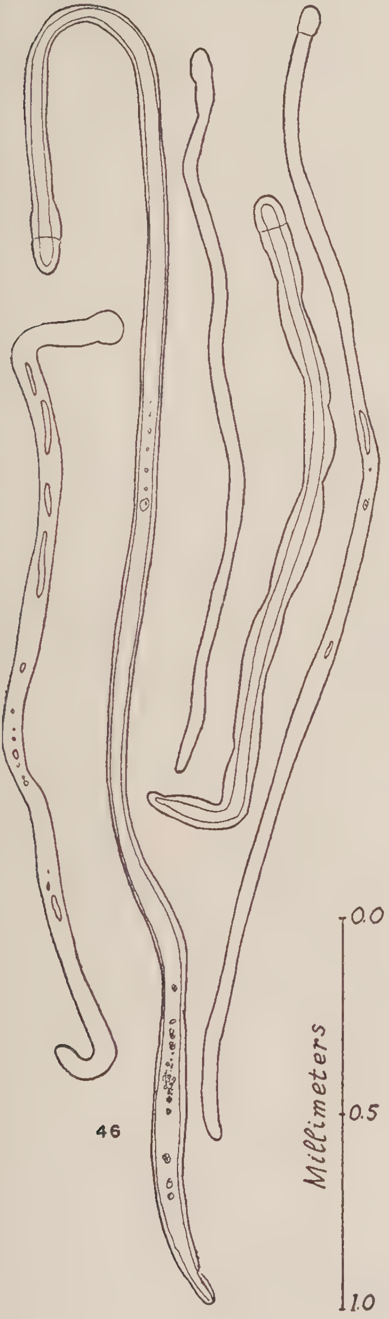
Fig. 46. *Dicyema balamuthi,* from off Point Loma, San Diego County, California.

Fig. 47. *Dicyema balamuthi,* from small octopus in the San Francisco Bay area.

Fig. 48. *Dicyema apollyoni.*

Fig. 49. *Dicyema acciaccatum.*

Fig. 50. *Dicyema acheroni.*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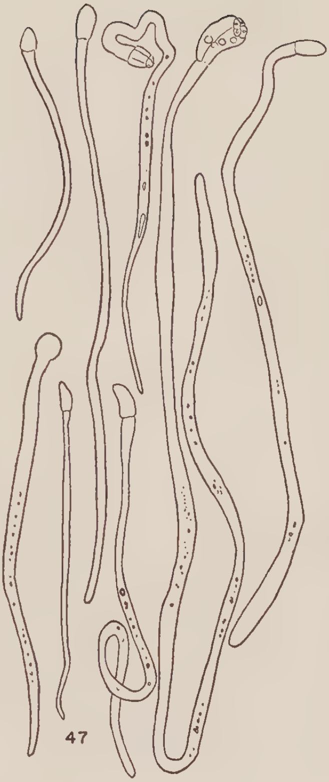

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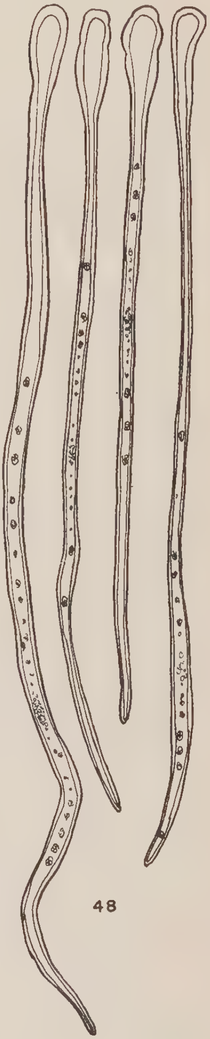

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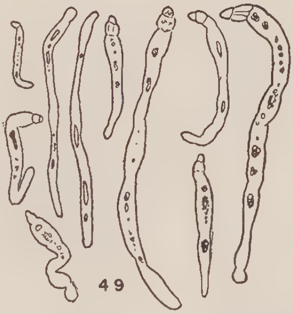

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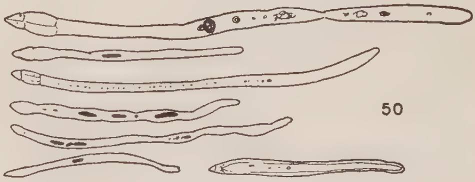

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PLATE 5

Figs. 51–55 *Dicyema apollyoni*

Fig. 51. Anterior end of a mature rhombogen (scale B).

Fig. 52. Anterior end of another rhombogen. Amitotic division of nuclei of some of the trunk cells indicated (scale B).

Fig. 53. Anterior end of a rhombogen (scale B).

Fig. 54. Portion of a transitional individual showing some enlarged fusiform germ cells (scale B).

Fig. 55. Vermiform larva (scale C).

Figs. 56–64 *Dicyema balamuthi*

Fig. 56. Anterior end of a transitional individual from off Point Loma (scale A).

Fig. 57. Anterior end of transitional individual from off Point Loma. Note inequality of parapolar cells common in this species (scale A).

Fig. 58. Elongated calotte, individual from San Francisco Bay area (scale A).

Fig. 59. Elongated calotte, individual from off Point Loma (scale A).

Fig. 60. Anterior end of nematogen from San Francisco Bay area (scale A).

Fig. 61. Anterior end of another nematogen from San Francisco Bay area with slightly elongated calotte (scale A).

Figs. 62–64. Vermiform larvae (scale C).

Figs. 65–67 *Dicyema acciaccatum*

Fig. 65. Anterior end of a rhombogen (scale B).

Fig. 66. Young primary rhombogen with some binucleate axoblasts (scale C).

Fig. 67. Young individual showing amitotic division of the axial nucleus into several parts (scale C).

Figs. 68–70 *Dicyema acheroni*

Fig. 68. Anterior end of a rhombogen (scale A).

Fig. 69. Anterior end of another rhombogen (scale A).

Fig. 70. Anterior end of a nematogen (scale B).

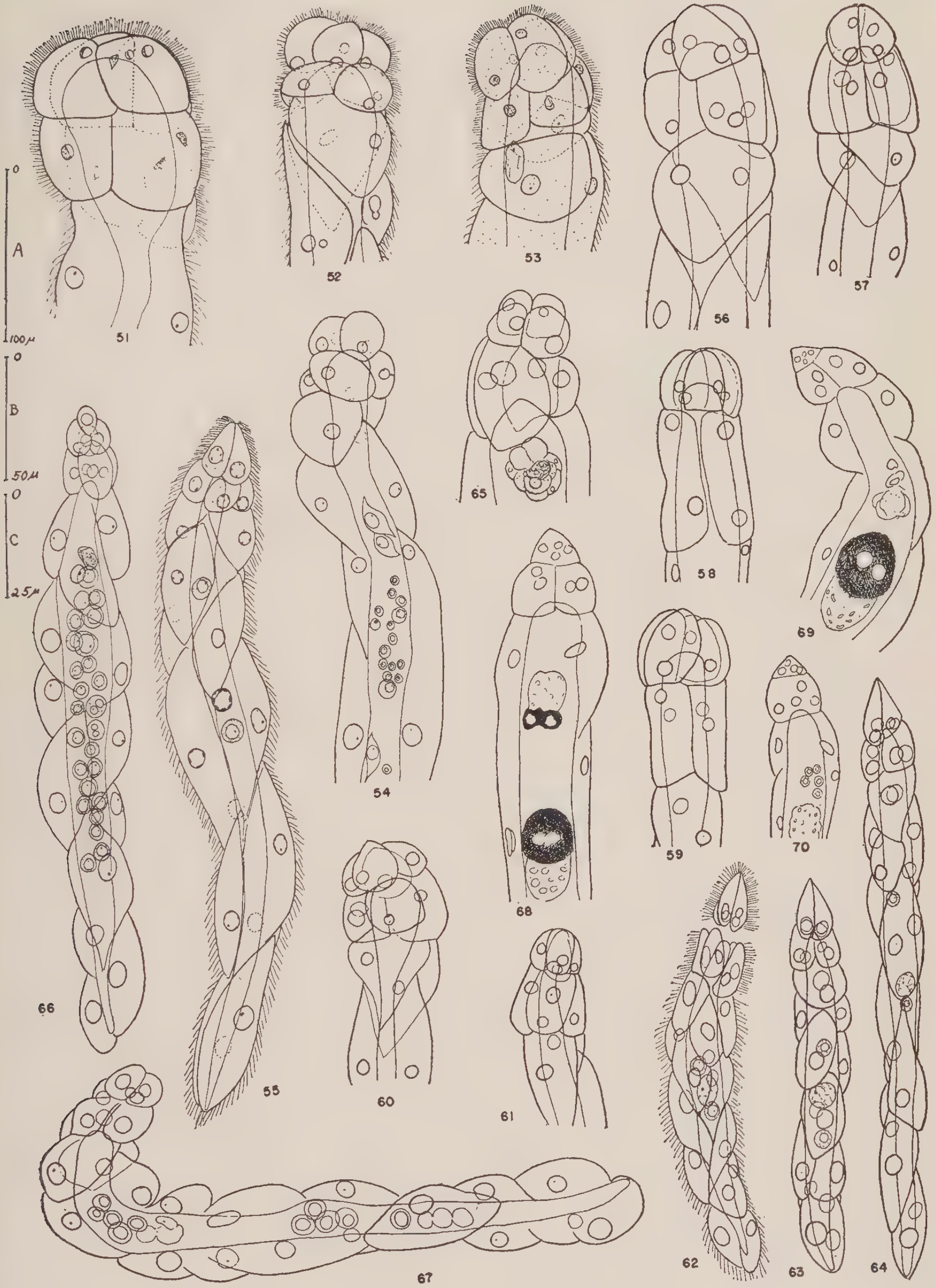
A
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PLATE 6

The Stem Nematogen of *Dicyema balamuthi*

Fig. 71. Larval stem nematogen with only the axial nucleus and one axoblast in each axial cell. A number of pycnotic remnants of larval abortive cells are still present undergoing absorption in the anterior somatic cells.

Fig. 72. Young stem nematogen. Some multiplication of axoblasts has taken place and the abortive elements have been completely absorbed.

Fig. 73. Another young stem nematogen of about the same age.

Fig. 74. Stem nematogen in which the development of larval primary nematogens has started. The two posterior axial cells each contain two fully formed larval primary nematogens.

Fig. 75. Mature stem nematogen containing a large number of fully developed larval primary nematogens in each axial cell.

Fig. 76. Anterior end of the individual shown in fig. 75, to show the flattened calotte, the three parapolar cells and their relation to the axial cell.

Fig. 77. Very large mature stem nematogen with numerous larval primary nematogens in each axial cell.

Fig. 78. Younger stem nematogen in which all 26 somatic cells show clearly.

Fig. 79. Anterior end of the individual shown in fig. 78, showing the calotte and the three parapolar cells.

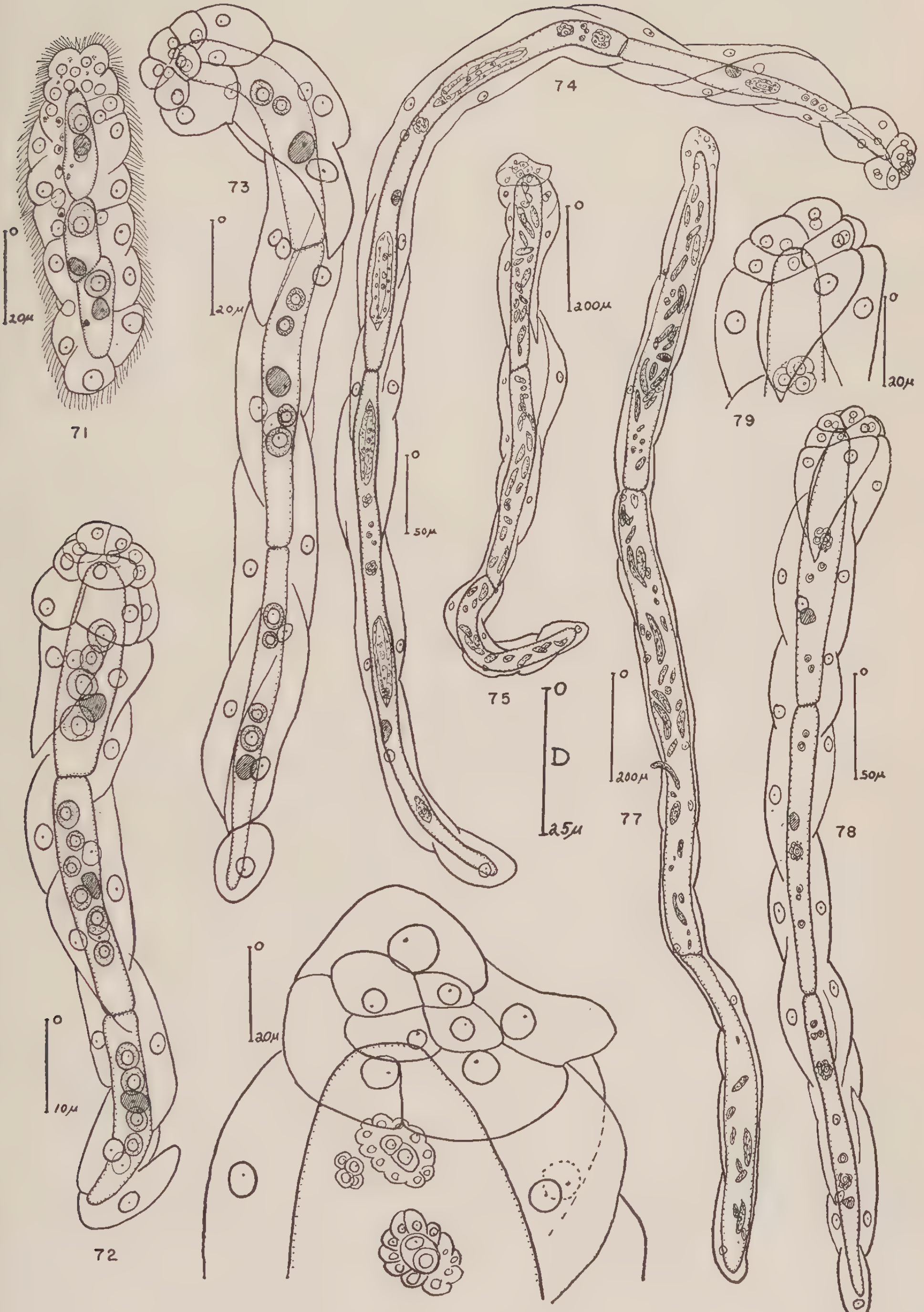
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PLATE 7

The Basis for the Genus *Dicyemodeca* Wheeler
Abnormalities of the calotte

Fig. 80. Anterior end of a nematogen of *Dicyemennea californica* with six metapolar cells (scale A).

Fig. 81. One of the many normal vermiform larvae contained in the axial cell of the nematogen figured in fig. 80, showing a normal calotte of four propolar and five metapolar cells (scale B).

Fig. 82. Anterior end of an individual of *Dicyemennea abelis* with six metapolar cells (scale A).

Fig. 83. A very young *Conocyema adminicula* with six metapolar cells (scale B).

Fig. 84. Anterior end of a rhombogen of *Dicyemennea granularis* with six metapolar cells (scale A).

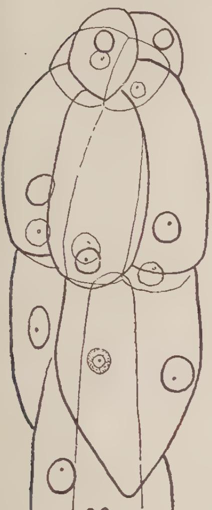
Fig. 85. Anterior end of a rhombogen of *Dicyemennea californica* with six metapolar cells (scale A).

Fig. 86. Anterior end of *Dicyemennea californica* with five propolar and five metapolar cells (scale A).

Fig. 87. Anterior end of *Dicyemennea californica* with five propolar cells, one of which is not well integrated with the calotte but shoved up between the propolar and metapolar cells (scale A).

Fig. 88. Larval *Dicyemennea californica* with five propolar cells. The parent nematogen and other larvae present were normal (scale B).

Fig. 89. Anterior end of a rhombogen of *Dicyemennea granularis* with five propolar and six metapolar cells, each set having been increased by one (scale A).



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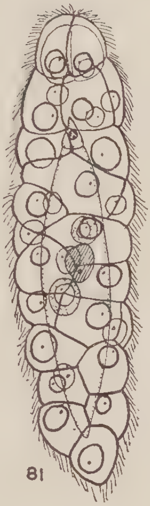

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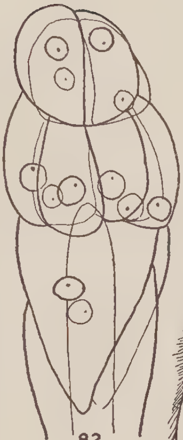

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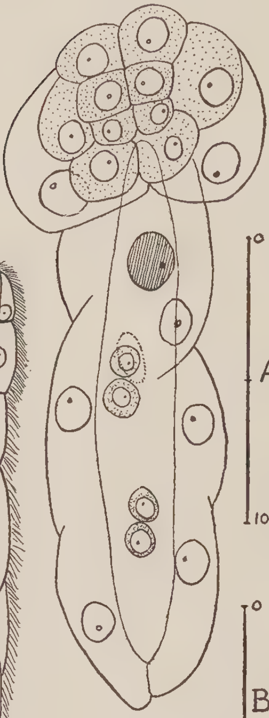

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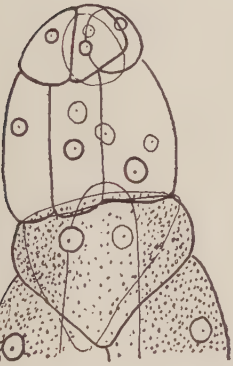

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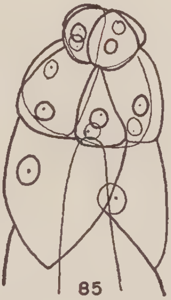

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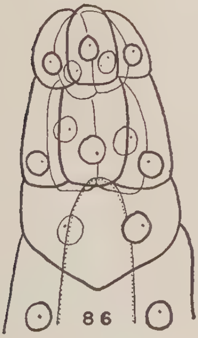

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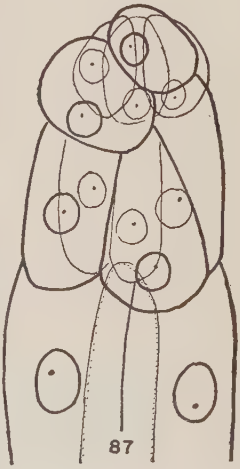

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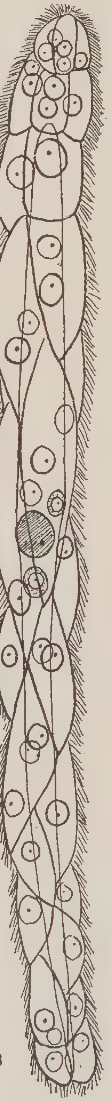

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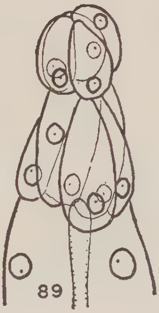

89

0
A
100 μ
0
B
30 μ

Contribution No. 425

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Thermal Control of Marine Fouling at Redondo Steam Station of the Southern California Edison Company

By W. L. CHADWICK,[1] F. S. CLARK,[2] and D. L. FOX[3]

The idea of controlling marine fouling by elevating the temperature of the sea water is not new, but it is felt that the application of this means of control in the cooling-water tunnels at the recently constructed Redondo Steam Station of the Southern California Edison Company at Redondo Beach, Calif., contains some features of interest. It is the object of this paper to describe the system employed and to present the results obtained during the first year of operation.

Design Considerations

PRIOR to designing the Redondo Station, it had been observed at the company's Long Beach Station that, whereas heavy fouling growths occurred in the intake tunnels, no serious fouling growths occurred in the discharge tunnels, even though these had never been cleaned in the history of the plant. The only difference in the tunnels to which this freedom from growth could be attributed was the higher temperature of the water in the discharge lines. In designing the Redondo Station, it was decided to utilize this condition to the maximum extent practicable, and also to provide facilities for chlorinating the water in the lines should treatment by higher temperatures not be fully successful.

The Redondo Station is situated on a section of sea coast that is exposed to winter storms and resultant heavy wave action. Hence it was highly desirable to have no structure offshore which would rise above the water and be subjected to pounding by large waves. Also, the beach at the plant site is one of the most popular in Southern California, and consequently no structures could be used that would interfere with the recreational use of the beach by the public.

These considerations precluded the use of a trestle or other structure to support chlorinator lines and a tower at the seaward end to house the chlorine apparatus, but led to the suggestion that two separate submerged lines be constructed out into the sea each of which could be used alternately as an intake or discharge, controlled by flow-reversing gates located on the shore end of the lines.

Thermal Sensitivity of Marine Fouling Animals

Biochemical control measures are commonly employed in combating marine fouling. These may involve the application of toxic paint surfaces to immersed structures such as ships' hulls, or the introduction of chlorine, organic chlorides, or other poisonous solutes into the moving streams of an enclosed system.

However, in an electric power-generating steam plant, utilizing flowing ocean water for cooling its condensers, a rather unique opportunity is offered for an introduction of a biophysical control feature, namely, heat. Two large tunnels at the Redondo plant of the Southern California Edison Company, each 10 ft ID, and extending for nearly 1900 ft into the open sea, are employed as intake and discharge channels, being alternated in these two functions at intervals of 2 to 4 weeks, depending upon the fouling season. Thus the periodic discharge of sea water through each tunnel at elevated temperatures has prevented the growth of fouling animals which have been observed in systems not accorded this treatment.

Experiments at the Scripps Institution of Oceanography reveal the fact that numerous sedentary marine invertebrate animals possess relatively sharp temperature-tolerance thresholds. Sedentary marine algae have not been investigated here, since they fail to colonize dark environments, and hence do not constitute a part of the fouling communities therein. Mussels, barnacles, sponges, tunicates, bryozoa, tube-worms, and anemones constitute the chief sources of trouble. In the Redondo and San Diego areas, the common mussel, *Mytilus edulis*, is the most prevalent member of fouling communities in sea-water tunnels. Barnacles, sponges, and tunicates are secondary foulers, while the large California mussel, *Mytilus californianus*, is an occasional invader at localities employing water from the open sea as distinguished from bays and estuaries which support only the other species, *Mytilus edulis*.

It has been found that the bay mussel, *Mytilus edulis*, is more resistant to exposures in warmed sea water than are *Mytilus californianus*, the barnacles *Balanus tintinnabulum*, *Balanus glandula*, the anemone *Cribrina xanthogrammica*, and other forms. *Mytilus edulis* is exceeded in this respect only by the small ribbed mussel, *Septifer bifurcatus*, but the latter species is so small and relatively sparse in numbers it does not constitute a serious threat.

In order to define working conditions which should hold promise for the practical thermal control of fouling, we therefore selected *Mytilus edulis* as representative of the most populous and relatively resistant fouling organisms common to these waters. Groups of young individuals (about 5–10 mm long, some 3–4 weeks old) were separated carefully and immersed in sea water at closely controlled temperatures for designated lengths of time. At the end of each experimental period, the animals were returned to running sea water and observed for possible survival. Survivors soon part their shells moderately, filter currents of sea water through their siphons, and attach themselves to solid surfaces by spinning the tough threads of adhesive byssus in the normal manner. Thermal casualties part their shells in a gaping fashion, die, and undergo decomposition of the flesh.

The following data have been collected relative to young specimens of *Mytilus edulis:*

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Note: Statements and opinions advanced in papers are to be understood as individual expressions of their authors and not those of the Society. Paper No. 49—S-13.

Temperature, deg F	Thermal death time, hr
106	0.33 (20 min)
100	1
95	6–7
90	13
85	41
82	96
77	Survive indefinitely

A graph of the foregoing data yields a smooth exponential curve. It is believed that swimming or freshly settled mussel larvae, being without shells, metabolically active and relatively more sensitive to unfavorable environmental factors, doubtless succumb more readily than do the young individuals which have formed their shells and undergone growth. Thus plant practice, guided by the foregoing data in the Southern California area, provides a generous margin of safety, especially provided that (1) at the height of the marine reproductive season (i.e., from early spring to late fall), water flow is alternated sufficiently frequently (at least every 2 to 4 weeks) to affect the larval or juvenile animals before they have had time to become firmly established, and (2) that temperatures within the upper range are maintained for the periods correspondingly indicated.

Moribund mussels reveal their condition in several observable ways, e.g. (1) by gaping, (2) by failure to close their valves upon mechanical stimulation (tapping the shell), (3) by failure to spin byssus strands for attachment, and (4) by decomposition of their fleshy parts. Even if any or all of the first three diagnostic signs are observable in a treated lot of mussels, it is invariably essential to remove the batch of animals and place them in a container of running sea water at normal temperatures. This was always done in our procedure, by having each lot of ten animals in a large porcelain vessel with perforated bottom (a large Gooch crucible).

At the end of an experimental period, a crucible of experimental animals was removed, drained of water, and the mussels were transferred immediately into a container of fresh cool sea water. This latter container, covered by a screen, was then placed in a running sea-water aquarium, and the experimental animals thereafter were observed during periods of several days. Some heat-narcotized sluggish animals later revive under these conditions, spin byssus, and propel water normally through their valves. On the other hand, some small mussels which fail to reveal their death by parting their valves, actually may be found to have died in this condition, the shell hinge being insufficiently rigid to operate conspicuously.

Observations always were continued on all animals given heat-treatment for a defined interval and then restored to natural conditions, until such time as we were able to determine that all died as a result of the heat, or that one or more survived. Thus sometimes the data are not all available for 3 or 4 days after the initial thermal treatment. Our data are all plotted on the basis of 100 per cent mortality.

With the use of this method of collecting reliable data, for example, we were able to obtain typical information relative to a series of mussels exposed to a temperature of 35 C or 95 F as shown in Table 1.

The time of 7 hr was manifestly the approximate period to be adopted as the lethal period for mussels of the indicated size and locality, exposed to a temperature of 95 F. Had we merely observed the condition of our animals in the experimental heating vessel, we should have been unable to collect reliable time data for lethality. The believed lethal period thus might exceed the actual lethal period by several or manyfold.

Manifestly the size range of experimental animals, the manner of heating and supplying reviving conditions, and clearly defined criteria of irreversible heat narcosis, leading to certain death, should all be standardized by experimenters in the field.

The definite possibility remains that mussels or other fouling species may vary somewhat in their thresholds of thermal tolerance, according to temperatures prevailing in their normal habitats. Marine animals living on the coast of the Pacific Northwest, for example, might be expected to manifest greater sensitivity, i.e., succumbing at less elevated temperatures and/or within shorter time intervals, than members of the same species, but possibly constituting a separate "physiological race," inhabiting Mexican waters. The sensitivity of races found at intermediate latitudes probably would lie between two such extremes. These matters should be borne in mind, and should be tested experimentally when contemplating the use of flowing sea water from any given region.

TABLE 1 THERMAL DEATH TIME OF MYTILUS EDULIS[a]

Date of start. 7-27-48 Time of start. 2.00 P.M. Nominal temperature 35 °C. or 95 °F.

Sample No.	Total No. per sample	Time heated		Temp °C.	Active			Indeterminate				Gaping				% Dead
		Clock	Exp.hrs.		7/28	7/29	7/30	7/28	7/29	7/30	7/31	7/28	7/29	7/30	7/31	7/31
1	10	5:00	3.0	34.7	1	10	10	9	0	0	0	0 (some sluggish)	0	0	0	0
2	10	6:00	4.0	34.7	0	4	7	10	6	1		0 (sl)	0	2		20
3	10	7:00	5.0	34.8	0	0	2	10	3			0 (sl)	7	1		80
4	10	8:00	6.0	35.2	0	0	1	10	1			0 (9 sluggish)	9			90
5	10	9:00	7.0	35.3	0	0	0	10				0 (all sluggish)	10			100
6	10	10:00	8.0	35.3	0	0	0	10				0 (all sluggish)	10			100

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[a] From records of D. L. Fox.

Description of Circulating-Water System

Reference is made to Fig. 1 which shows the facilities for withdrawing water from the Pacific Ocean for the Redondo Station. Two 10-ft-ID precast concrete pipes are laid in the floor of the beach in trenches, having a minimum earth cover of 4 ft, and extend into the sea for a distance of about 1900 ft. The lines were constructed under water by the use of divers, and facilities for unwatering the lines are not provided. The terminal structures are vertical precast concrete towers 14 ft diam, extending about 10 ft above the sea floor and protected by a rock riprap. The top of these towers is about 20 ft below mean lower low water. They are separated laterally by 200 ft to avoid recirculation of the water.

The choice of pipe internal diameter was selected as 10 ft after considering such factors as cost, flow, and possible decrease in diameter by marine growths, with attendant increase in roughness factor. The present pipes will be adequate to handle all the circulating-water requirements for the plant when the latter is expanded to its present ultimate capacity of 264,000 kw. At this load the circulating-water requirement will be about 180,000 gpm.

The shore end of each concrete pipe is connected to a concrete structure in which there are four vertical steel gates which can be raised or lowered with electric motors. The gates are arranged and operated so that one of the concrete pipes acts as an intake and the other as a discharge conduit. At intervals, the position of the gates is changed so that flow is reversed in each conduit. In this way either conduit may be used alternately as a discharge or intake.

Other equipment in the shore structure includes a discharge chamber for warmed water returning from the main condensers in the power plant, a trash rack for collecting and removing seaweed and other trash, revolving screens for removing fish and other marine growth, a suction chamber for the main circulating-water pumps, and a pump house. Circulating water for the main condensers is conveyed from the pumps through 54-in-ID precast concrete pipes laid underground. The latter are not subjected to the antifouling treatment to be described later because it was possible to provide access to them for periodic cleaning by manual means whenever it becomes necessary to do so. Antifouling measures are applied to the two 10-ft-ID pipes under the ocean principally because of their inaccessibility for the usual methods of cleaning.

There is also provided in the pump house equipment for chlorinating the circulating water. Chlorine can be introduced into the water at two places and for two purposes as follows:

1 At the circulating-water pump intake as a desliming agent for the condensers.

2 At the shore end of the 10-ft-ID discharge pipes as a toxic agent for killing marine organisms in the pipe. So far the latter use of chlorine has not been necessary due to the success of the method to be described.

Flow Reversal

The reversal of the circulating water is effected by four vertical gates, one located in each intake and two at the outlets of the transfer basin or reversing chamber. The gates normally will operate in pairs, one intake and one discharge opening, the other pair closing. Gates are 7 ft wide and 10 ft high, built of fabricated steel. They are provided with cast manganese-bronze guides with bronze sealing strips and with stainless-steel stems. The four gates normally operate together at uniform speed, 4 min being required for the complete stroke. The gate hoists are operated electrically, and the position of each is remotely indicated on both the circulating-water panel board in the steam station and the chlorination control panel on the second floor of the chlorination building.

During the 4-min period of reversal there will be a certain amount of recirculation of warmed water, from that gate which has been the discharge and which is now closing, to the intake, which has been closed and which is now opening. The flow in that tunnel, which has been the discharge, is gradually reversing, and some warmed circulating water will be drawn back into the intake. The effect of the reversal of the circulating water is shown in Fig. 2 in which the elevation of the free water level in the forebay has been plotted against elapsed time following the start of the gate movement. This curve sheet is based upon a circulating-water flow of 400 cfs and on a tide level of 0.0. It will be noted that the water level in the intake basin starts at approximately 3 ft below grade 0.0 (which is the head loss in the intake tunnel) and reaches a maximum low grade just after the gates have completed reversal. This lag is a result of the time required to decelerate and reverse the flow of water in the intake tunnel. Approximately 14 min are required for the re-establishment of equilibrium at a level of 3 ft below grade 0.0 (corresponding to the head loss in the discharge tunnel), and a peak water level of approximately 8.5 ft above grade 0.0 is reached just after the completion of the gate movement.

The foregoing maximum and minimum levels are based on an ocean grade of 0.0, corresponding to mean lower low water. When a low tide at —2.5 or a high tide at 7.0 ft occurs, these tide levels below and above grade 0.0 must be superimposed on the level variation shown in Fig. 2. Additional hydraulic data are shown in Table 2.

A weir has been provided at grade 16.0 in the top of the east wall of the transfer basin. Should simultaneous occurrence of

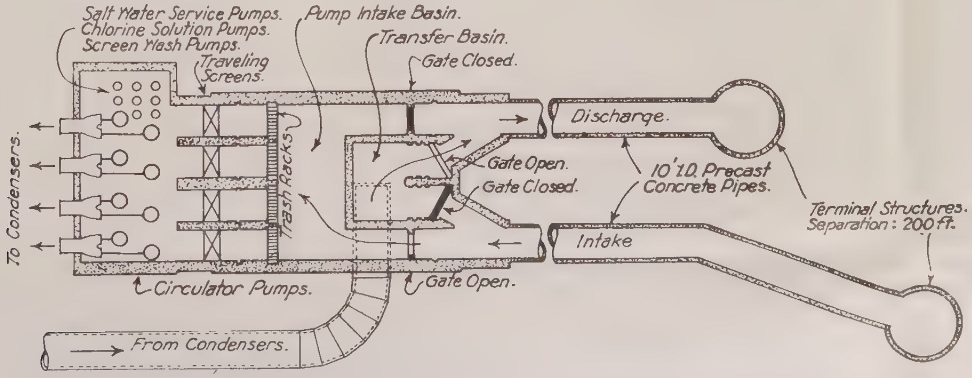

Fig. 1 Facilities for Withdrawing Water From the Sea for the Redondo Station

TABLE 2 ELEVATIONS, HYDRAULIC GRADIENT, AND HEAD LOSSES OF CIRCULATING WATER SYSTEM, REDONDO STEAM STATION

Elevations: (Mean lower low water = 0.0)	
Top of intake and reversing-chamber structure	15.0 and 18.5
Bottom of intake and reversing-chamber structure	−19.0
Top of overflow weir reversing chamber	16.0
Bottom of screen well and pump well	−22.0
Pump-house floor	5.28 and 15.0
Circulating-pump intake bell	−19.16
Steam station basement floor	10.0
Center line of condenser intake	18.5
Top of condenser tail pipe	25.0
Center line of 10-ft discharge tunnel-condensers to reversing chamber	−2.5 and −2.0

Hydraulic gradient: (Based on a flow of 400 cfs with allowance for marine growth on tunnel walls)	High water (7.0)	Mean lower low water (0.0)	Low water (−2.5)
Level in intake basin	3.7	−3.3	− 5.8
Minimum level of intake basin, during period of flow reversal	...	...	− 9.8
Level in pump well	2.4	−4.6	− 7.1
Minimum level in pump well, during period of flow reversal	...	...	−11.1
Level in reversing chamber	10.3	3.3	0.8
Maximum level in reversing chamber, during period of flow reversal	15.8	...	...

Head losses: (With allowance for marine growth on tunnel walls)	Two units, 200 cfs	Four units, 400 cfs
Alternating intake and discharge tunnel (L = 2007 ft)	0.8 ft	3.3 ft
Screen wells	0.6	1.3
Inlet-pipe line, pumps to condenser	4.8	4.8
Condenser	16.9	16.9
Discharge pipe line, condenser to reversing chamber	7.9	9.8
Alternating intake and discharge tunnel (L = 1825 ft)	0.7	2.7
Total	31.7	38.8

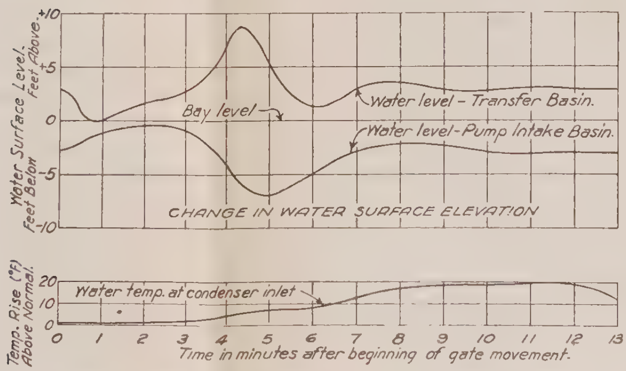

FIG. 2 EFFECT OF REVERSAL OF CIRCULATING WATER

maximum flow, flow reversal, and high tide cause this basin to overflow, the excess water will discharge into the intake basin.

For a short period following tunnel reversal, condensers will receive warmer than normal circulating water owing to the recirculation which occurred when all four gates were open and changing, and to the reversal of the flow in that tunnel which had been the discharge and which became the intake. Fig. 2 indicates that a temperature rise above normal may persist for some 12 min, with a peak rise of 19 deg F prevailing for 3 min. This calculated rise of inlet-water temperature above normal is based upon a heat rejection of 1720 × 10^6 Btu per hr to the circulating water corresponding to the extreme conditions of four units operating at 66,000 kw. For any lower station load, the magnitude of this temperature rise will be proportionally reduced. It has been found by experience that the reversal cycle does not affect the ability of the main units to carry full load.

ELECTRIC CONTROL OF REVERSING GATES

Each of the four gates is provided with an electric motor operator and means for automatic and manual position control. Automatic control, under which all four gates operate in sy chronism, two opening and two closing, is derived from t chlorination control panel. A manual switch for positioni the four gates synchronously is located on the chlorinati panel, while local switches permit the positioning of individu gates. A position indicator for each gate is located on th chlorination control panel and the circulating-water panel the steam station.

Indicating lights are provided at the chlorine control boar and at the motors to show the position of the gates. Re indicates gate fully open. Green indicates gate fully close Red and green together indicate gate is either moving or stoppe in an intermediate position.

After a gate-positioning operation has been initiated, shoul an obstruction or a power failure cause any one of the gates t stop before completion of one half of its travel, all gates revers their travel and are restored to the same position as befor operation was initiated. In case the gates have completed mor than one half of their travel before one gate stops, all othe gates complete the operation. An alarm will sound at the circulating-water gage board if gates go out of synchronism.

BASIS OF PRESENT TREATMENT

The marine fouling organisms which are particularly troublesome at this location are as follows:

1 Bay mussel (*Mytilus edulis*).
2 Large sea mussel (*Mytilus californianus*).
3 Barnacles (*Balanus tintinnabulum* and *Balanus glandula*).
4 Hydroids.

Laboratory investigations at the Scripps Institution of Oceanography, University of California, indicated that, of those organisms listed, *Mytilus edulis* is the most prolific and resistant to elevated temperatures, and therefore that any temperature found to be lethal for *Mytilus edulis* would also prove to be fatal for the others. Accordingly, further experimentation to determine the effect of temperature and time of exposure was confined to this mussel as it was abundant and convenient.

The result of the laboratory work is shown in Fig. 3. The curve indicates that this mussel can survive indefinitely at temperatures below 77 F. However, at temperatures above 82 F, survival is dependent upon the time of exposure and, after a temperature of 100 F is reached, the mussel dies within 1 hr.

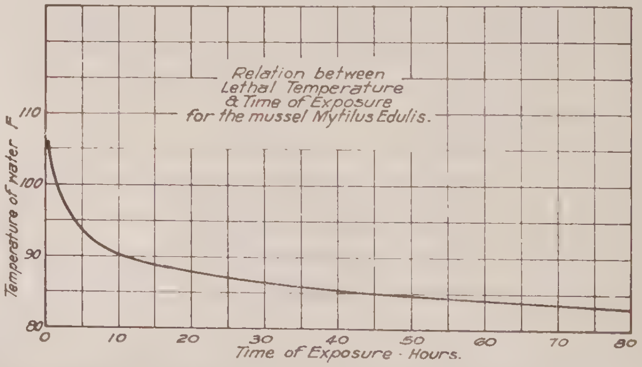

FIG. 3 RELATION BETWEEN LETHAL TEMPERATURE AND TIME OF EXPOSURE FOR THE MUSSEL, MYTILUS EDULIS

The reproductive cycle of this mussel practically ceases during the winter months when the ocean temperature drops below 60 F, and new mussels do not appear in troublesome numbers until the water temperature increases beyond 60 F in the late spring. Accordingly, it is believed that little or no treatment will be required during the winter dormant period. Conclusive evidence on this point will not be available until further experience with the system has been obtained.

The information in Fig. 3 is applied to the problem of keeping the pipes free of marine organisms in the following way: During the months when the ocean water exceeds 60 F, the gate positions are reversed periodically, causing a reversal of flow in the two lines so that the line which acted as the intake line becomes the discharge line. As soon as this happens, the temperature of water in the line increases about 19 deg F if full load is being carried in the plant. Depending upon the ocean-water temperature, this is increased further by opening one of the gates partially to cause recirculation of the water to the condenser until the temperature of the water flowing in the discharge pipe is raised to about 102 F. As shown on the curve in Fig. 3, the mussels cannot survive this temperature for longer than 1 hr. To make certain that all mussels and other growths are killed, it has been the practice, during the first summer season that this method has been tried, to maintain this temperature for 4 hours before restoring the gate to normal position and stopping recirculation.

The function of the pipes has been reversed and the temperature of the water increased as just mentioned at varying intervals from 10 days to 3 weeks. It appears that once every 3 weeks may be sufficient and, as later experience with this method develops, it may be possible to increase the length of the interval between flow reversals.

RESULTS

During the summer of 1948 the pipes and terminal structures were treated as outlined, and during this time they remained completely free of any fouling organisms. To check upon the effectiveness of the method, a diver was employed to examine the interior of the pipes and terminal structures at least once a month and oftener during the initial phases of the operation. Also, removable concrete test panels about 1 ft × 3 ft were hung in the pipes to provide a spot sample for any growths which might have accumulated. These were removed periodically for examination above water, and likewise were found to be free of troublesome growths throughout the first summer period.

Effectiveness of the method also has been demonstrated in another way. Referring to Fig. 1, in the pump intake chamber there are located, in addition to the main circulator pumps, several small vertical pumps used for station salt-water service. During the latter part of the first summer's operation, it was necessary to raise these for internal inspection, and it was found at that time that the external surface of the pump columns carried a layer of mussels about 6 to 8 in. thick below the water line. The water surrounding these pumps does not receive the full heat-treatment given to the main conduits, and therefore the mussels are not killed periodically but flourish instead in their unmolested environment. It is reasonable to expect that growths of similar magnitude might have accumulated in the main conduits during the same period had not the treatment described in the foregoing been used.

COST OF TREATMENT

The operating cost of the treatment is relatively small when the benefits derived are evaluated with it. It is also small when compared to the alternative method of using chlorine in lethal quantities to perform the same service. No exact data are available for the latter method because, so far, it has not been necessary to employ the method. However, an estimate has been made of the probable cost of using chlorine rather than heat and is reported here for comparison.

During the 4-hr period when the water temperature is elevated artificially at the expense of condenser vacuum and, consequently, fuel cost, the vacuum drops approximately 1 in. Hg. On an annual basis, it is estimated that the heat-treatment costs about $800 for the two 66,000-kw turbine generators presently installed. Based upon the best available estimates rather than the actual use of chlorine to accomplish the same results, if such were possible, it is expected that the annual cost of chlorine would be about $50,000.

While it is true that some additional capital expenditure was necessary to provide the facilities for reversing the flow of water periodically, it is judged that the fixed charges on these are considerably below the annual expense for chlorine as just estimated.

CONCLUSION

A system has been devised for controlling the troublesome growth of marine organisms in two concrete ocean-water conduits by elevating the temperature of the discharge water periodically for short periods to a value slightly in excess of 100 F. The scheme has worked well during the first year of plant operation and has done so at a cost believed to be much lower than with the use of chlorine.

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DANGEROUS CURRENTS IN THE SURF

DANGEROUS CURRENTS IN THE SURF

by Francis P. Shepard

Rip currents, not undertow, can sweep the unwary swimmer seaward. Knowing how to spot these rips, and what to do if caught in a strong one, may help a swimmer save his life.

Surf bathing leads to the drowning of thousands of people each summer. "Caught in the undertow" is the usual explanation for these disasters and yet there may be no such thing as undertow. In dictionaries it is defined as "the current beneath the surface which sets seaward when waves are breaking on the shore." Many geological textbooks contain brief discussions of undertow, ascribing it to the seaward return of landward driven surface water.

No actual measurements have been made con-

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Ewing Galloway.

Ewing Galloway.

firming the existence of dangerous subsurface currents of this nature. Our extensive investigations at Scripps Institution, both in the surf zone and outside the breakers, have to date shown no appreciable seaward movement of water along the bottom in areas where the surface current was setting landward. In fact, the net movement at the surface is ordinarily in approximately the same direction as it is at intermediate depths and even near the bottom.

Rip Currents Described

There is another type of dangerous seaward movement for which there is abundant confirmation and which is well known to lifeguards on beaches where there is large surf. This has been called rip tides or sea pusses, but rip currents or rips are more appropriate names because the currents have nothing to do with tides nor, of course, with seagoing pussy cats. These rip currents differ from the hypothetical undertow in that they extend from the surface of the water to the sea bottom both inside the breakers and for some distance outside. Farther out they are confined to the surface and intermediate depths and thus ride over the bottom water quite the opposite of the hypothetical undertow.

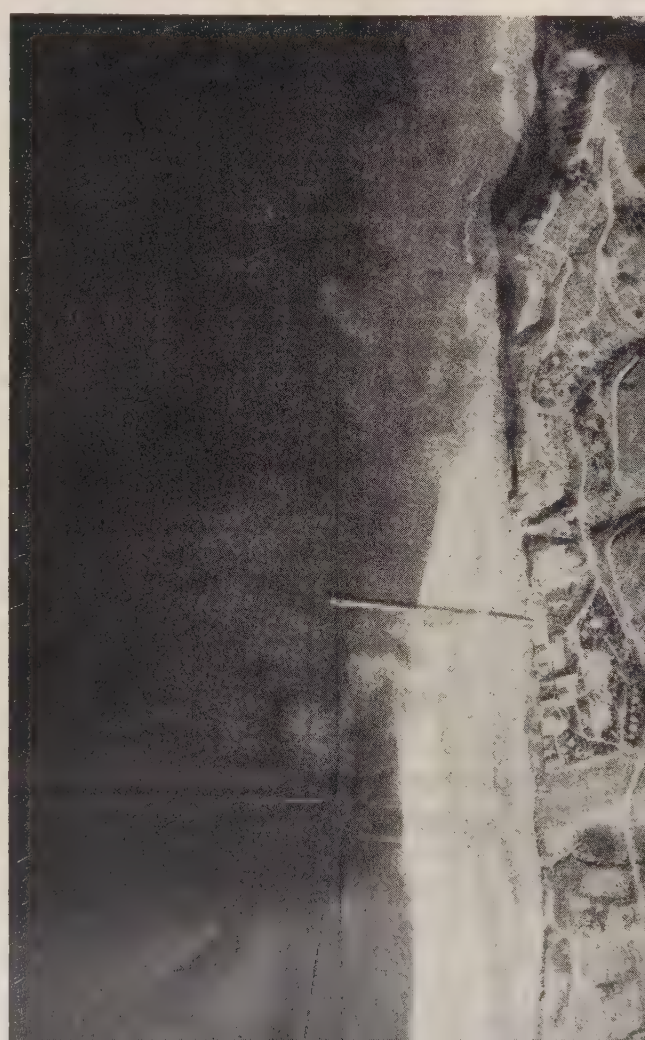
These currents move out in narrow bands through the breakers and spread slowly into fan shapes beyond. Between the seaward flowing masses there are broader areas where the water moves towards the land more slowly than the rips move seaward. The shoreward drift also extends from top to bottom of the water column in most places. The result of this shoreward drift is to build up water along the shore with a resultant flow parallel to the shore. These longshore currents are deflected seaward into rip currents.

Rip currents are easy to spot from the air. They can also be seen by a practiced eye from the beach. Whenever there are large waves approaching more or less directly towards a relatively straight beach, one can detect their presence. On clear days it is a rare occasion when we are unable to see them from the upstairs windows of the Scripps Institution which commands a view of the open Pacific. From the air or from any position where you can look down on the surf, rips can be distinguished by the turbulent brownish or greenish masses of water which are moving out from the breaker zone, having somewhat the form of a cauliflower cloud rising from a volcano, or of a thunderhead. The flow is intermittent so that one mass follows another somewhat like puffs of smoke from an engine. The edge of each advancing rip is likely to be outlined by foam which has been carried out from the surf zone.

Viewed from the beach, rips can be detected by the turbulence of the water along the lanes of flow or by a change in color of the water in the surf zone where the rip current or its feeding longshore current has eroded the bottom and thus varied the absorption of the light due to the suspended sediment and to the depth. This same channeling effect may prevent the breaking of the wave as it moves shoreward leaving a gap in the breaker line. If the wave does break in the rip zone, the typical brownish color of the water can be seen in the breaking wave.

The rates of flow in rip currents have not been

Rip currents from the air. Note widening of surf zone in lower portion of picture. Variation is related to submarine canyon which comes in close to coast in the zone of inconspicuous surf. Rip currents are pronounced near margins of wide surf zones. Scripps Institution photo.



Rip currents, seen from Scripps Institution pier, are indicated by foam streaks extending out in two gaps in the breaker line.

Scripps Institution photo.

measured under extremely large breaker conditions, but it can be safely assumed that they increase with increase in the size of the waves. Numerous observations when the waves were small (less than about three feet high) indicate that in general rips are so gentle in flow that they are scarcely felt by swimmers. Where the waves attain heights of four feet or more, the currents are likely to be troublesome. With somewhat larger waves, currents of two or three miles an hour have been measured.

In the surf zone, rip currents have a different effect on floating objects which extend partly above the surface than on objects which are slightly submerged or on patches of sea-marker dye. Objects floating on the surface are ordinarily carried seaward as far as the line of large breakers, but then are often thrown shoreward again when they rise into the crest of the breakers, so that they move around in eddies near the breaker line and have little net transport. Sea-marker dye or submerged floats, on the other hand, will move readily through the breakers with only temporary pauses accompanying the passage of large waves.

The reason that a floating object is often stopped at the breaker line can be explained by considering the Hawaiian sport of surfboarding. The transverse profile of an advancing wave crest approaching the breaker line becomes asymmetrical, steepening towards the shore. As a result floating objects, such as surfboards, rise on the steep side of the advancing wave crest and slide down the steep forward slope under the influence of gravity. Thus, in the absence of outflowing currents the net move-

ment of the object is shoreward. In a rip current the shoreward sliding of a floating object tends to offset the seaward movement of the current. It is because of this surfboard action that even a weak swimmer may not be carried through the breakers although he may have extreme difficulty in getting out of the influence of the rip current. On the other hand a drowning man who has become submerged will go out through the breakers without interference.

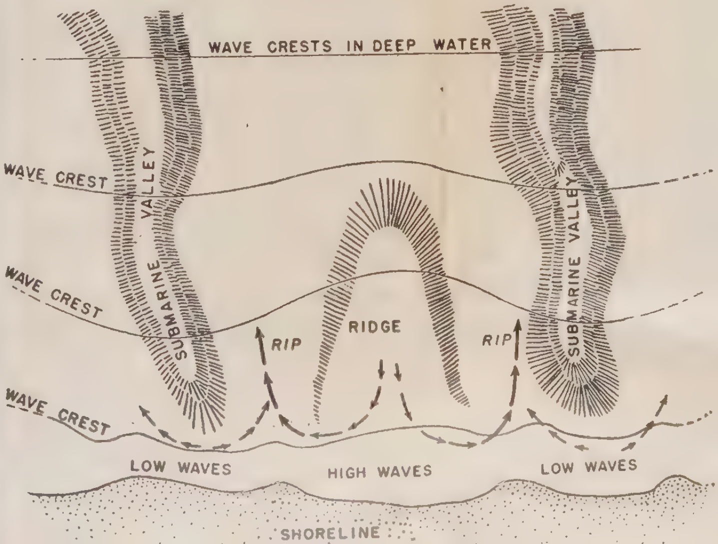
Black Star.

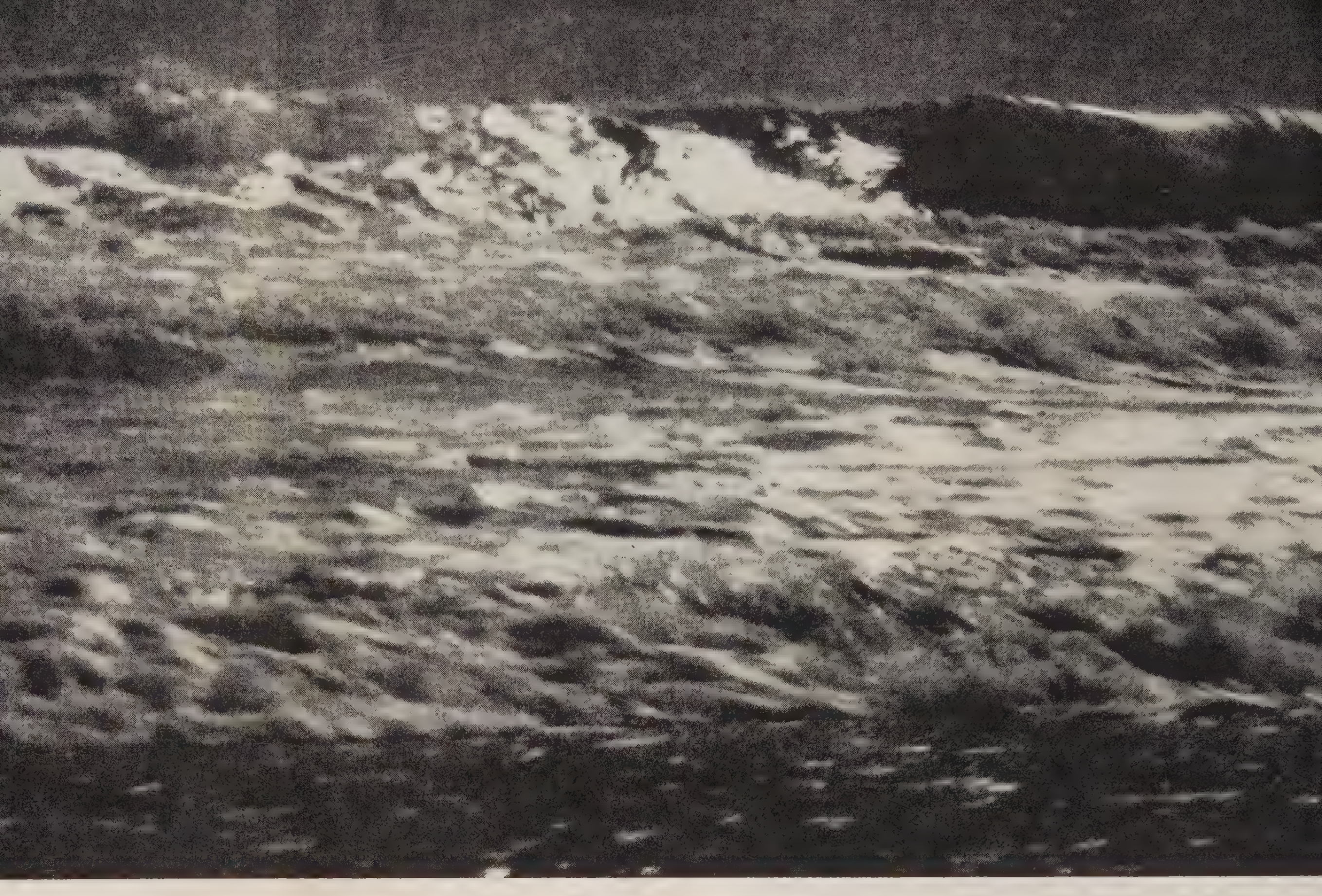
Rip Currents Explained

The explanation of these near-shore currents appears to be the same as the explanation which was formerly offered for the hypothetical undertow. They are the result of the net shoreward movement of particles of water in waves. The effect of this motion is to pile up water along the shore. As a result there must be net return flow seaward which equalizes the shoreward mass transport. This return could take place underneath the surface or it could take place in restricted lanes both at and below the surface. The evidence now available, as we have already indicated, favors the second of these alternatives.

There are several factors which tend to localize the return flow (that is, the rip currents). Probably the most important of these influences is what is known as wave convergence. Where an even wave crest, moving towards shore from deep water, encounters a sea floor irregularity, even of a very minor nature, the crest is bent. If the irregularity is a shoal or a ridge, the crest is held back and the wave becomes concave towards the shore. If the irregularity is a deep, such as a submarine valley, the crest is bent in the opposite direction since it moves faster along the deep valley than on the shoaler sides. The effect of the ridge is to converge the wave energy and thus cause the waves to increase in height, whereas the effect of the valley is to spread the energy and decrease the wave height.

Inside a ridge or any small bottom projection, the shoreward transport of the water particles is intensified. Near the breaker line this shoreward movement extends from top to bottom although the velocity decreases downward. The next effect of the convergence is to build up water to a greater height shoreward of convergences than elsewhere. This de-

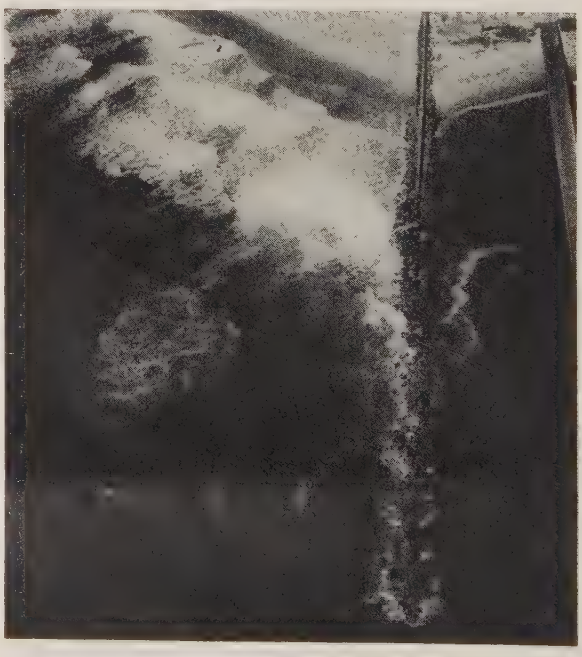




velops a gradient which produces longshore flow away from the zone of convergence on either side. These longshore currents in turn become rip currents where they can break their way seaward. The outflow may occur spasmodically near the point of convergence, but a much more regular outflow occurs outside the area of the highest waves where there is less of the shoreward mass transport to interfere with the outflow.

Measurement of the velocity of rip currents has shown a distinct relation to groups of high waves which ordinarily alternate with groups of low waves. Contrary to a popular concept, the large waves do not come as the seventh wave in a series but at very irregular intervals depending on the times when two or more series of waves of different period and source happen to have coinciding crests. Directly after the large waves break, the water is piled up along the shore resulting in either a strong longshore flow and a resulting strong rip, or an outflow near the point of raised sea level. Because of the lag in developing the return flow, the maximum currents in the rips generally occur during the times of the smaller waves.

Another location in which rip currents are common is on the up-current side of an obstruction (for example, the north side of a pier during south flowing currents). Diagonally approaching waves develop a longshore current in the direction in which they are advancing (except in the case of wave convergence already discussed). These longshore currents turn seaward at obstructions such as projecting points of land. As a result very large rips are



Development of rip current on the up-current side of a jetty.
Scripps Institution photo.

Ewing Galloway.

often seen extending seaward for thousands of feet on one side of a prominent point. Jetties cause similar rips, and even piers are likely to have a rip on one side although they do not offer as much interference to the longshore flow as do the solid structures.

At the head of a submarine canyon, where the waves are generally much reduced, the convex approach of the wave crests results in an impinging of waves on the shore so as to push the water away from the canyon head. The feeble longshore currents are deflected seaward as rip currents when they approach the much stronger rip currents flowing away from the wave convergence area at some distance from the canyon head. These two rip currents join on the outside of a triangular area of quiet water. Inside these triangles the shoreline generally projects seaward due to the deposition of a sand point.

Advice to Surf Bathers

It is not always easy to apply advice on methods of escaping from dangerous rip currents, particularly when a poor swimmer has been carried out beyond his depth. His first consideration should be to keep away from rips. But one has little to fear from dangerous currents along the open coast, where tidal currents are unimportant if the breaker heights are low—that is, less than about three feet. (To test this height one can stand knee deep in water, during upsurges, and see if one can observe the horizon over the top of the advancing breakers. The method will not work if the wave breaks far out from shore.)

If the breakers are large the poor swimmer should keep in shallow water, never getting deeper than waist height, even during the largest waves. He should also avoid bottom irregularities, which indicate the existence of channels cut by the feeder currents of rips. Even if the water in the channels appears to have little current a series of large waves may send a great concentrated surge along the channel, sweeping the bather off his feet and out into the zone of large breakers.

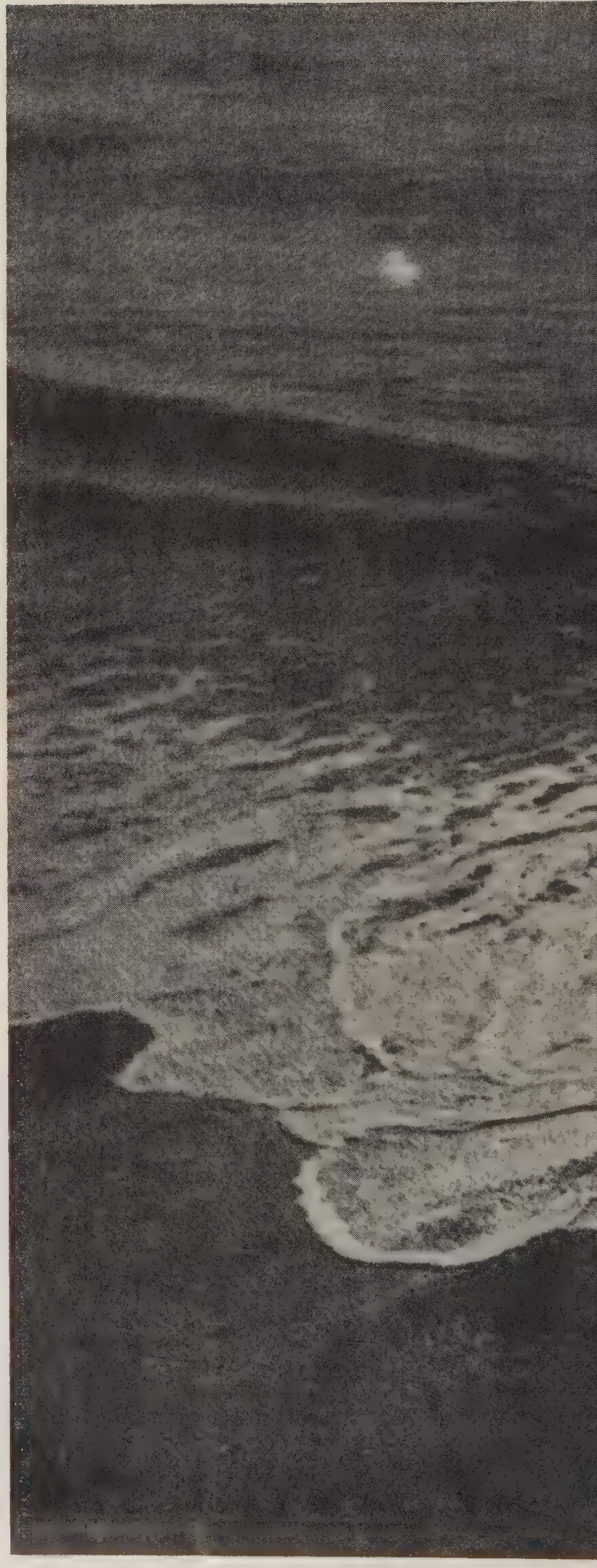
For the swimmer of moderate ability who does get caught in a rip current, the most important advice is to conserve his strength and not to try to force his way shoreward against a powerful surge. Swimming at right angles to the current will almost always allow the swimmer to get out of the rip channel so that he can touch bottom in the shoal water on either side. If the swimmer finds it difficult to get out on one side because large feeder currents are coming in on that side, he should turn around, and swim parallel to shore in the other direction.

It is important also to remember that the advancing breakers can prove very helpful unless they threaten to plunge down directly on top of you. As such a breaker approaches, the swimmer should swim under it in order to avoid being plunged to the bottom with great violence and then driven seaward during the return flow. A good swimmer can ride in on the front of the advancing breakers, even in a rip current, but this is not wise for most bathers. Unless the breaker is of threatening proportions, one should try to get high enough on the advancing front to receive at least a temporary shove towards shore.

If a swimmer is carried out through the breakers by a powerful rip, as happens not infrequently, he should swim parallel to the shore far enough to be able to come in on the side of the rip where he will generally find a favorable current. However, he should guard against being caught in the feeder currents which flow parallel to the shore and may sweep him back into the rip. A feeder current like a rip current varies in intensity. Therefore the swimmer can wait in the comparatively shallow water outside the feeder channel until the current slackens before making the crossing.

It is often possible for a moderately good swimmer to rescue someone in distress in the outer breaker zone by swimming out to him and finding a sufficiently shallow spot nearby so the man can stand up at least during wave troughs. The rescuer may then help the victim or encourage him to swim to the shallow area where he can rest his feet on bottom between wave crests.

There is no doubt but what most drownings take place simply because the bather loses his head and struggles with such violence that he becomes exhausted or has a heart attack. Relaxation and natural buoyancy will get even poor swimmers out of many serious predicaments. One should never forget that the rip currents are spasmodic and that the strong flows are generally of short duration, a few minutes at the most; the belts in the breakers are narrow so that a few strokes may take one clear of the danger area.



Black Star

Contribution No. 427

JOURNAL OF SEDIMENTARY PETROLOGY, VOL. 19, NO. 2, PP. 51–70
FIGS. 1–5, AUGUST, 1949

SORTING OF SEDIMENTS IN THE LIGHT OF FLUID MECHANICS

DOUGLAS L. INMAN

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ABSTRACT

Observations show that a physical relationship exists between the sorting, skewness and median diameters of sediment samples. Investigation of the fluid mechanic principles involved in the transportation and deposition of sediments indicates that there are three primary controlling factors; the degree of bottom roughness, the settling velocity, and the threshold velocity. Analysis of sedimentary processes in the light of these controlling factors indicates that the relationship of sorting and skewness to the median diameter of a sediment may furnish a clue to the conditions under which the sediment was transported and deposited.

INTRODUCTION

It has frequently been observed that both the sorting and skewness coefficients from a suite of sediment samples are a function of the median diameter of the sample. This fact is well illustrated by Hough's (1942) samples from Cape Cod Bay, by Shukri and Higazy's (1944) Red Sea sediments, and by Krumbein and Aberdeen's (1937) Barataria Bay sediments. In all cases, samples having median diameters near .18 mm are the best sorted; the sorting coefficient increasing in magnitude for median diameters greater or less than .18 mm. The Cape Cod and Barataria Bay samples also show a definite relationship between the skewness coefficient and median diameter. In addition, the dependency of sorting and skewness coefficients upon median diameter has been observed frequently by the author in the analyses of beach and bottom sediments in the southern California region. Visual best fit curves of the plots of sorting coefficients and logarithms of the skewness coefficients versus median diameters for the Cape Cod Bay, Barataria Bay and Red Sea sediments, and for some southern California beach sands, are shown in figure 1.

The description of sediments by the parameters,[1] geometric median diameter *Md*, coefficient of sorting *So*, and coefficient of skewness *Sk*, (or by their equivalent in phi units) is a statistical description analogous to the median, standard deviation, and skewness of mathematical statistics. These parameters are based on the quartile measures Q_1, *Md*, and Q_3 obtained from the cumulative frequency curve of the mechanical analysis of the sediments. *Md* is defined as the diameter in millimeters of the middlemost member of the cumulative frequency curve; such that 50% by weight of the sample is larger and 50% smaller. The first quartile measure, Q_1, is that diameter having 75% of the sample smaller and 25% larger; the third quartile, Q_3, is that diameter having 25% of the sample smaller and 75% larger.

The sorting coefficient (Trask, 1932) is defined as

$$So=\sqrt{\frac{Q_1}{Q_3}}$$

and the skewness coefficient as

$$Sk=\frac{Q_1Q_3}{Md^2}\,.$$

Both *So* and *Sk* are dimensionless, and while physically they appear to be related to the median diameter, this relationship is not implied in their definitions.

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[1] All symbols are defined in "Notation and Dimensions" at the end of the paper.

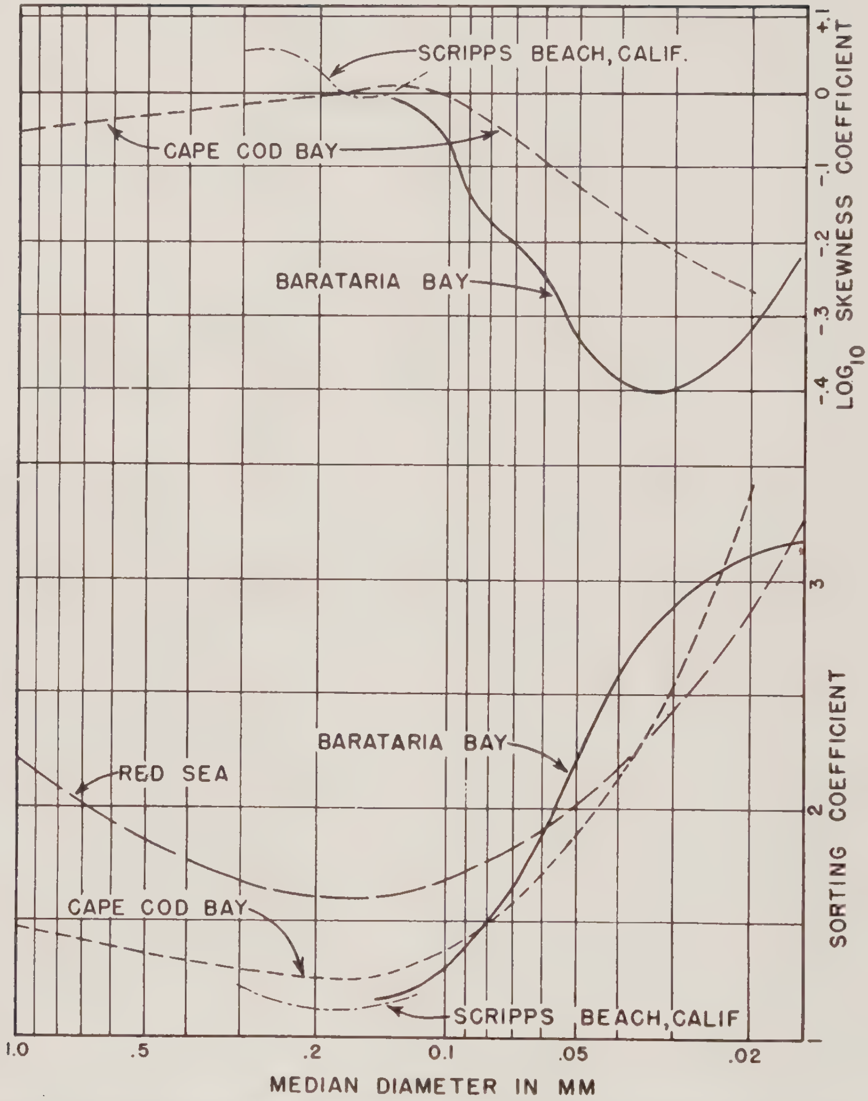

FIG. 1.—Relationship of sorting and skewness coefficients to median diameter of Cape Cod Bay, Barataria Bay, and Red Sea sediments, and Southern California beach sands.

If the histogram of a sediment is skewed towards the fine grade sizes (i.e., the median is finer than the mode) *Sk* will have a value less han 1.0; if it is skewed towards the coarse grades *Sk* will be greater than 1.0. *Sk* will have a value of unity for a symmetrical size distribution of sediments.

The values and interrelationships of these statistical parameters are a complex function of the nature and strength of the transporting agent, the amounts and types of sediment available for transport, the distance transported, and the resulting boundary layer conditions between the transporting medium and the bottom.

It is the purpose of this paper to examine these relationships in the light of fluid mechanics.

ACKNOWLEDGMENTS

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HYDRODYNAMIC RELATIONS

Some of the more pertinent relationships of the boundary layer theory are discussed below. Readers interested in a more complete development are referred to general fluid mechanics texts (for example, Rouse, 1938).

Boundary Layer: Meterologists have investigated boundary layer problems pertaining to the atmosphere and hydraulic engineers have conducted experiments on such problems in flumes, but the results must be modified before being adapted to the ocean or to natural streams.

In general, natural water flows are inherently turbulent in their upper reaches. It should be remembered that while it is customary to describe a turbulent flow by the average velocity $\bar{u}$, the velocity at any instant, u, is the vector sum of the average velocity and a random fluctuation related to turbulence. This may be written

$$u=\bar{u}+u'. \tag{1}$$

The flow conditions near the boundary surface can be considered by examination of a vertical section based at the bottom of a natural stream. Assume a horizontal bottom with a current flowing in the x-direction, and the average horizontal velocity, $\bar{u}$, a constant for any given depth during the period of our investigation. If the bottom is considered to be hydrodynamically smooth, there will be a thin layer of laminar flow on the bottom even though the main flow be inherently turbulent. If the surface be hydrodynamically rough, then the turbulence effectively extends to the very bottom.

Flow in the laminar layer is characterized by the absence of random velocity fluctuations. In flow of this type, thin fluid layers are considered as moving parallel to each other in such a manner that the viscous stress τ exerted on a unit surface between these layers, the shear normal to that surface du/dz, and the coefficient of molecular viscosity μ, are related by Newton's fundamental equation

$$\tau=\mu\frac{du}{dz}. \tag{2}$$

An equation analogous to (2) may be written for the condition of turbulent flow:

$$\tau=A_z\frac{d\bar{u}}{dz} \tag{3}$$

where $\bar{u}$ is the average velocity and A_z is the value of the eddy viscosity A, applicable in the vertical direction. "A" is the exchange coefficient introduced by Schmidt (1917) as a result of the space exchange of momentum due to random fluctuation in turbulent flow. Both μ and A have the dimensions of $ML^{-1}T^{-1}$. It should be noted that the molecular viscosity is independent of the state of motion and is a characteristic property of the fluid. Observations show that the eddy viscosity is not a constant in natural currents, but depends upon the nature of the fluid movement. The eddy viscosity is many orders of magnitude larger than the molecular viscosity. For ocean currents A has been found to range between one and 1000 c.g.s. units (Sverdrup, *et al.*, 1942, p. 91).

Prandtl's Mischungsweg Theory leads to a definition of A_z as

$$A_z=\rho l^2\left|\frac{d\bar{u}}{dz}\right| \tag{4}$$

where l is the "mixing length," ρ is the density of the fluid, and $|d\bar{u}/dz|$ is the absolute value of the shear. Over a rough surface l must have a definite value, since turbulence extends to the very bottom, and for a fluid of indifferent stability may be written

$$l = k_0(z+z_0)$$

where k_0 is von Kármán's constant, and has been found to be equal to nearly 0.4. z is measured positive upwards, and z_0 is the roughness length and is related to the height of the roughness elements.

Combining equations (3) and (4) and considering the stress to be constant, one obtains the von Kármán-Prandtl equation for boundary currents over a rough surface:

$$\text{(5a)} \qquad \bar{u} = \frac{u_*}{k_0} \ln \frac{z+z_0}{z_0}$$

where the factor u_* is equal to $\sqrt{\tau/\rho}$ and is called the "friction velocity." u_* has the dimensions of a velocity and is proportional to the average velocity $\bar{u}$. A coefficient γ is defined by

$$u_* = \gamma \bar{u}$$

and comparison with equation (5a) shows that γ is a function of the height at which $\bar{u}$ is measured above the bottom, and the degree of bottom roughness. Munk (1947) has reviewed the evidence which indicates that γ has a constant value over a rough surface, and decreases abruptly in magnitude at a critical wind speed below which the surface becomes smooth.

Equation (5a) gives the average velocity as a straight line function when plotted against the logarithm of $z+z_0$ and enables u_* and z_0 to be obtained from the slope of the velocity gradient and the z-axis intercept.

For a smooth surface equation (5a) is not applicable. The von Kármán-Prandtl equation for the velocity distribution in turbulent flow over a smooth surface is

$$\text{(5b)} \qquad \bar{u} = 5.5u_* + \frac{u_*}{k_0} \ln \frac{u_* z}{\nu}$$

where ν is the kinematic viscosity, μ/ρ.

The stress in turbulent flow may be written (von Kármán, 1935) in the Reynolds form as

$$\tau = -\rho \overline{u'w'}$$

where u' and w' are the random velocity fluctuations in the x and z directions respectively. If it assumed that a correlation exists between u' and w', then the friction velocity is proportional to the mean of the absolute value of the velocity fluctuations. Further, if one assumes the turbulence to be isotropic, the friction velocity is equal to the mean of the absolute value of the velocity fluctuations

$$u_* = \sqrt{\frac{\tau}{\rho}} = \overline{|u'|} = \overline{|w'|}\,.$$

Roughness Criterion: From von Kármán's Law for flow over a smooth surface the thickness of the laminar layer may be written

$$\text{(6)} \qquad \delta = \frac{\lambda \nu}{u_*}$$

where λ is a constant. It seems logical to assume that if the bottom is to be considered rough, the roughness elements (sand grains for example) must protrude above the laminar layer. This assumption suggests that some constant value of the ratio of bottom grain diameter d to the thickness of the laminar layer may be a criterion between rough and smooth bottoms. If one substitutes the value of δ from equation (6), the ratio d/δ may be written in the dimensionless form of a Reynolds number:

$$\frac{u_* d}{\nu} = \text{constant.}$$

The experiments of Nikuradse (1933), Fage (1933) and White (1940) indicate that the criterion between smooth and rough surfaces is a critical value of the ratio u_*d/ν such that:

$$\underset{\text{rough surface}}{\frac{u_*d}{v}} > 3.5 > \underset{\text{smooth surface}}{\frac{u_*d}{\nu}} \cdot$$

One can therefore define a critical friction velocity $u_{*r} = 3.5\nu/d$ at which the character of the bottom changes from smooth to rough. This critical friction velocity will be referred to as the *roughness velocity.*

Settling Velocity: Newton (see Camp, 1946) proposed that a particle falling in a fluid will accelerate under the force of gravity until the "frictional drag" of the fluid approaches the value of the impelling force, after which a constant velocity c, called the settling velocity, will be reached. The frictional drag law was proposed on the assumption that the drag force F_D is proportional to the square of the velocity:

$$F_D = C_D B \rho \frac{v^2}{2} \tag{7}$$

where C_D is a dimensionless number called the drag coefficient; B is the projected area of the particle in the direction of motion ($\pi d^2/4$ for spheres); and v is the relative velocity between the particle and the fluid.

Instead of being constant as Newton assumed, the drag coefficient is found to be a function of the Reynolds number $R = vd/\nu$.

When a small particle settles in a fluid it is acted upon by a force of gravity acting downward, and by a buoyant force (given by Archimede's principle) acting upward. The difference between these two forces is called the impelling force. For spherical particles it is equal to $1/6\pi g \rho' d^3$, where g is the acceleration due to gravity, and ρ' is the difference between the density of the particle and that of the fluid.

By equating the impelling force to the drag force, the settling velocity is found to be;

$$c = \sqrt{\frac{4}{3} \frac{g}{C_D} \frac{\rho' d}{\rho}} \cdot \tag{8}$$

In the region of viscous settling (diameters smaller than .18 mm) C_D is equal to $24/R$. Substituting this value of C_D in equation (8) gives Stokes Law for settling velocities of small particles.

$$c = \frac{1}{18} \frac{g}{\mu} \rho' d^2.$$

Particles with diameters greater than .18 mm have settling velocities sufficiently great to cause turbulence to develop, and the settling velocity no longer follows Stokes Law. The settling velocity (from Rubey, 1933) is plotted against the particle diameter in figure 2.

A spherical quartz grain of .18 mm diameter has a settling velocity in water of approximately 2 cm/sec. It is interesting to note that the Reynolds number of the grain at this velocity is equal to the critical value of the bottom roughness criterion

$$\frac{u_*d}{\nu} = 3.5.$$

THEORY OF SEDIMENT MOVEMENT

There appear to be three distinct methods of transportation of sediments by currents: *surface creep*, *saltation*, and *suspension.* The first is a bed load phenomenon in which the material slides or rolls along the bottom with a velocity less than that of the fluid current. Saltation is a jumping motion in which the particles momentarily bounce above the bottom and travel with the velocity of the fluid.

The forces associated with currents that cause a particle to move have been explained in the following ways (Rubey, 1938): (1) by the impact or momentum of the water which strikes it, (2) by frictional drag on its surface, and (3) by differences in pressure induced by differences in current velocity.

The impact principle (giving the 6th

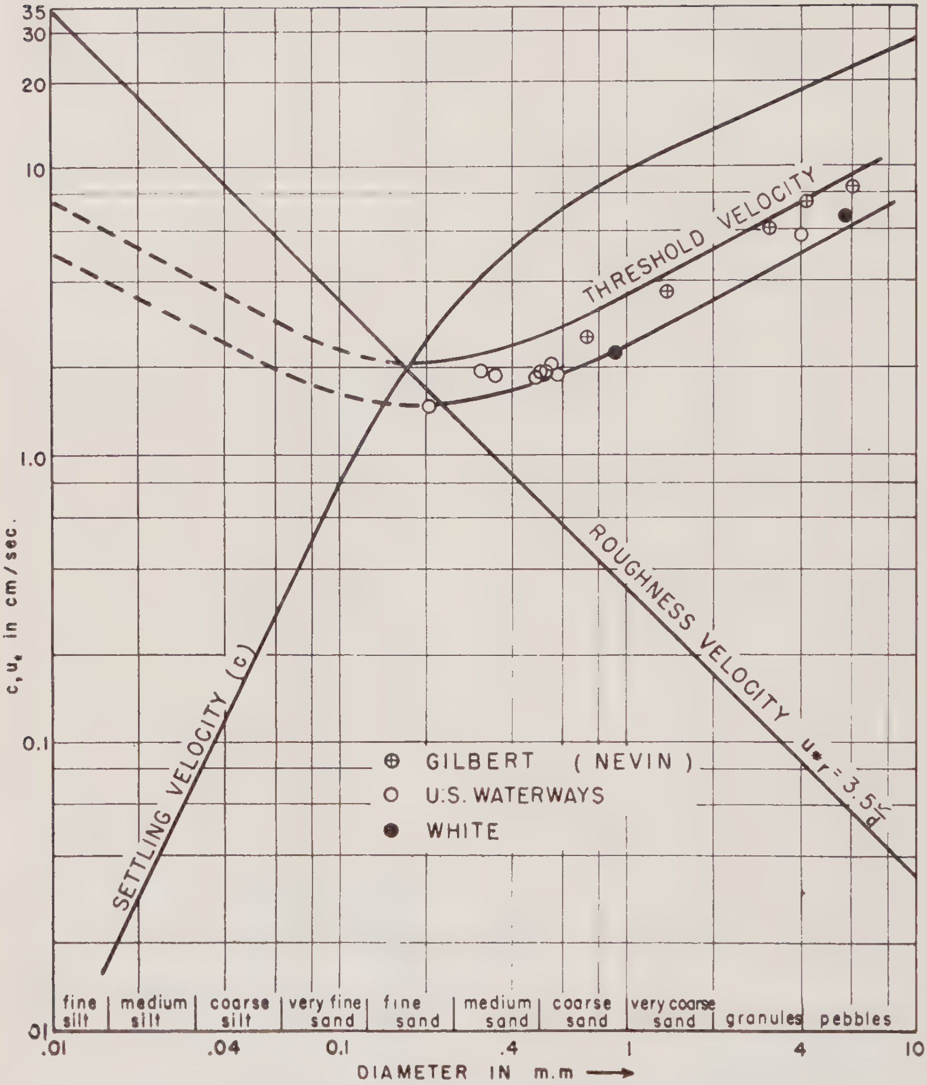

Fig. 2.—Relation of grain diameter to settling velocity, threshold velocity and roughness velocity.

power law) is difficult to evaluate in terms of bottom currents, since it necessitates measuring the current at the boundary surface. Consideration of frictional drag leads to the conclusion that a critical tractive force exists which is important to sediment movement.

Surface Creep: Experiments by Shields (1936), White (1940), Bagnold (1942) and others indicate that movement will not take place until a critical drag force that is a function of grain size is exceeded. The critical drag force f_c on a spherical particle may be written as

$$f_c = \alpha g \rho' d^3 \tan \phi$$

where α is a factor depending upon the type of flow, and ϕ is the angle of repose of the grains. If the sand is of uniform diameter d, the number of grains per unit area that are exposed to the fluid drag are p/d^2, where p is the packing coefficient and is defined as d^2 times the number of exposed grains per unit area. The critical drag force per unit area τ_c is equal to $f_c p/d^2$, or

$$(9) \qquad \tau_c = p\alpha g\rho' d \tan \phi.$$

The factor α is a function of the roughness criterion $u_* d/\nu$, and experiments show it to have a value of .25 for values of $u_* d/\nu$ greater than 3.5 (White, 1940). The critical drag may be expressed in terms of a critical frictional velocity u_{*c}

$$u_{*c} = \sqrt{\frac{\tau_c}{\rho}}\,.$$

This critical value of u_* at which sand movement starts, owing to the drag force of the fluid, is called the "threshold velocity" (Bagnold, 1942, p. 86).

We have dealt in general terms with a critical drag force or its equivalent threshold velocity which may be computed from the average velocity profile (see equation 5a). However, it should be remembered that if even momentarily the value of u_{*c} is exceeded, movement will result. Thus we are interested in the instantaneous velocity u, consisting of the average velocity $\bar{u}$, plus the velocity related to random fluctuation u' (see equation 1). Kalinske (1943) shows that the instantaneous drag force may be many times that computed from the average velocity.

A broad curve including some of the experimental values of the threshold velocity for various grain diameters is shown by parallel solid lines in figure 2. These threshold velocities were computed from the experimental critical drag forces obtained by White (1940), the U.S. Waterways Experiment Station, and from Nevin's (1946) analysis of data obtained by Gilbert. Since it is not always practical to measure velocity profiles in shallow water flume experiments, the critical drag forces in the above mentioned experiments were computed from du Boys' equation. This may be written in c.g.s. units as

$$\tau = g\rho Di$$

where D is the depth of flow and i is the slope of the bed. The bed slope is assumed to be equal to the slope of the water surface. The threshold velocity gradually decreases with decreasing grain diameter until a diameter of approximately .18 mm is reached. At this point the value of $u_* d/\nu$ becomes less than 3.5, the bottom becomes effectively smooth, and individual grains cease to shed small eddies. The drag, instead of being carried by a few grains, is more evenly distributed over the whole surface. As a result of these changes the velocity necessary to start surface movement increases as the grain diameter decreases below approximately .18 mm. This startling fact was experimentally demonstrated (Bagnold, 1937) by blowing a stream of air over a loosely scattered layer of fine Portland cement powder. It was found that no movement occurred even when the wind was strong enough to move pebbles 4.6 mm in diameter.

It should be noted that while the relationship $u_* = \gamma \bar{u}$ holds for a smooth surface as well as for a rough surface, the value of γ is not the same in both cases. The use of a constant value of γ in computing threshold velocity from the aveage stream velocity may not give accurrate values when the bottom changes from rough to smooth. However, the stream velocity required to move the finer material does increase with decreasing grain size for water as well as wind transported sediments (Hjulström, 1939). This fact is illustrated in figure 2 by dotted lines representing the *apparent* threshold velocity. The data for this section of the curve were obtained from average stream velocities tabulated by Hjulström (1935).

Saltation: As soon as movement of sand has been initiated, some of the particles may be lifted off the bed into the fluid stream. Once in the fluid stream, the particles acquire the velocity of the fluid and travel with it until gravity forces them back to the surface of the bed. The particle may "bounce," or strike another particle, causing it to leave the surface. Jeffreys (1929) has shown that the initial rise of particles from a bed may be partly explained on a basis of Bernoulli's principle giving a resultant upward force in the presence of a steep velocity gradient. Here again, u_* may become an important parameter since it is related to the velocity gradient.

Kalinske (1943) believes that saltation is not important in water, although it has been observed by Gilbert (1914), Bagnold (1942) and others. Certainly it loses its significance for fine-grain sediments.

Suspension: Transportation of sediment in suspension is a problem both in diffusion and advection. A qualitative relationship for material in suspension under conditions of equilibrium was first developed by Schmidt (1925) for air and later applied to silt in water by O'Brien (1933). Schmidt assumed that the mass of sediment particles carried downward by gravitational settling must equal the amount carried upward by turbulent motion. This relationship may be written in terms of the distance above the bottom z and the eddy viscosity A_z as

$$(12a) \qquad \ln \frac{S_z}{S_a} = -c \int_a^z \frac{dz}{A_z/\rho}$$

or, in terms of the velocities at these elevations and the friction velocity u_* as

$$(12b) \qquad \ln \frac{S_z}{S_a} = -c \int_a^z \frac{d\bar{u}}{u_*^2}$$

where S_z/S_a is the ratio of the concentration of sediment having a settling velocity c, at height z to that at a constant height "a."

The theory of the vertical distribution of sediment in suspension is dependent on a concentration gradient. It should be noted that under similar flow conditions, the ratio of the sediment concentrations is proportional to e^{-c}, where e is the base of natural logarithms. Thus fine material has a more uniform distribution with depth, and hence a smaller concentration gradient than coarse material. If the height "a" is considered to be infinitely close to the bottom, and the turbulence is sufficient to cause suspension, then the concentrations of the various grain sizes at height "a" are proportional to the amount of each grain size on the surface of the bottom.

The significance of the suspension equations may be better understood by further development of equation (12b). Integrating (12b) and using (5a) and (5b) we obtain

$$(13) \quad \log_{10} \frac{S_z}{S_a} = -\frac{1}{k_0} \frac{c}{u_*} \log_{10} \frac{z+z_0}{a+z_0} \cdot$$

Here $z_0=0$ corresponds to flow over a smooth surface.

If we assume that the particles in suspension are spherical, of diameter d, and of the same specific gravity, then the settling velocity of the particles (equation 8) is a function of d only: $c=f(d)$. Setting $u_*=nc$, where n is any positive number, we obtain

$$(14a) \quad \log_{10} \frac{S_z}{S_a} = -\frac{1}{nk_0} \log_{10} \frac{z+z_0}{a+z_0} \cdot$$

Equation (13) tells that if we select fixed values of z and "a," any curve for which the ratio u_*/c equals a constant is a curve along which the concentration ratio S_z/S_a is also a constant. In a coordinate system u_* vs. d we can therefore construct a family of curves for constant values of the concentration ratio. For the sake of simplicity we may select

$$\frac{z+z_0}{a+z_0} \doteq \frac{z}{a} = 10$$

and obtain

$$\text{(14b)} \quad \log_{10} \frac{S_z}{S_a} = -\frac{1}{nk_0} \qquad (\text{for } z = 10a).$$

It will be noted from equation (14b) that when u_* equals c, $n = l$ and

$$\log_{10} \frac{S_z}{S_a} = -2.5 \qquad (\text{for } z = 10a)$$

where k_0 is equal to 0.4.

This value of the logarithm of the concentration ratio will be used as the limiting value for which suspension is significant. In effect, this means that if suspension is to exist to a significant degree, then u_* must be equal to, or greater than, c; and under our arbitrary selection of elevations $z = 10a$, the logarithm of the concentration ratio must be equal to, or greater than, -2.5.

This selection is in agreement with an analysis of experimental data by Lane and Kalinske (1939, also Kalinske, 1941) which indicated that a value of unity for n, the ratio of the friction velocity u_* to the settling velocity c, is a criterion for the beginning of suspension. This criterion can also be justified on the basis that, since u_* is equal to the mean of the absolute value of the vertical turbulent velocity fluctuations $\overline{|w'|}$, it should be expected that a significant degree of suspension can exist only if the settling velocity is less than $\overline{|w'|}$.

A number of curves of constant concentration ratios are shown in figure 3. The limiting value of -2.5 for which suspension is significant is shown as a heavy line. This curve for which $u_* = c$ may also be interpreted as a plot of the settling velocity against the particle diameter d. It corresponds to the settling velocity curve in figure 2.

In the application of suspension to sorting and skewness frequent reference will be made to the settling velocity curve in figure 2 and to the role of settling velocity as a criterion for suspension. However, it should be remembered that the settling velocity curve is but one of the family of curves illustrated in figure 3, its significance being that it is the particular curve for which the threshold velocity is equal to the settling velocity.

APPLICATIONS OF HYDRODYNAMIC THEORY

Some of the many complex factors that enter into the problem of the interrelationships of sorting, skewness, and median diameter have been discussed above. It is necessary to consider the effect of these factors in both the transportation and deposition of sediments. In the laboratory, experiments have been performed under controlled conditions on various phases of the sedimentation problem, but in nature not only are the conditions far from being controlled, but the relative importance of the different factors is not clearly understood.

In figure 2, three parameters, the settling velocity, the roughness velocity and the threshold velocity, are plotted on double log paper with the velocity components c and u_* as the ordinate and the grain diameter in millimeters as the abscissa. These relationships are for spherical grains with a specific gravity of 2.65 in water at 20° centigrade.[1] It should be remembered that this graph is drawn for homogeneous grains of one size, and that studies of sorting and skewness involve aggregates of two or more grain

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[1] A preliminary inspection, not based on experimental data, indicates that the three curves in figure 2 will retain their general relationship for changing particle specific gravity (water being the fluid media). Since the roughness criterion is independent of the grain specific gravity, it will remain a constant. Material with a specific gravity greater than 2.65 will have a higher settling and threshold velocity, so that the three curves should intersect on the roughness velocity at a smaller grain diameter and a higher value of u_* and c. Theoretical calculations with grains of magnetite (specific gravity 5.17) gave an intersection of the curves in the very fine sand grade. For specific gravity less than 2.65, the three curves should intersect at a greater grain diameter and a smaller value of u_* and c.

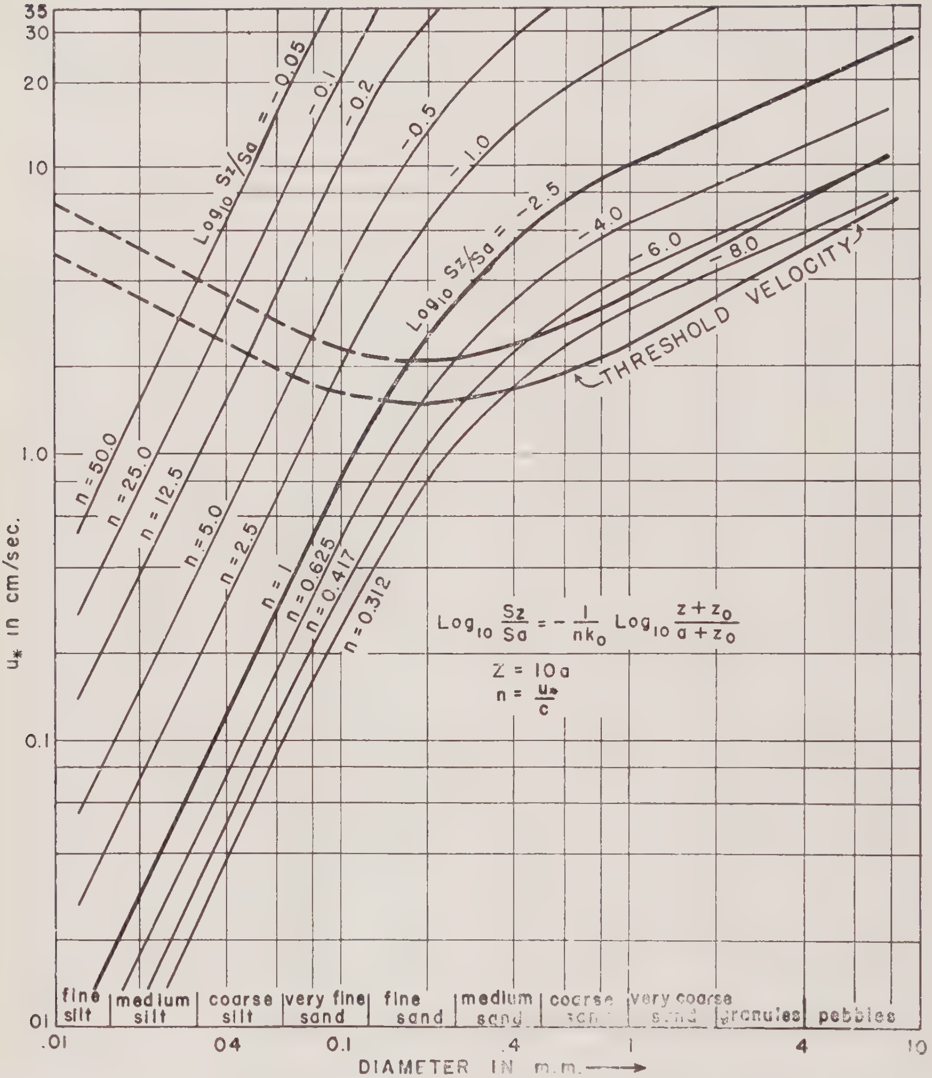


FIG. 3.—Relation of the concentration ratio of suspended material to the threshold velocity.

sizes. While the use of such a graph tends to over-simplify the true picture, it is hoped that it will serve to illustrate some of the fundamental characteristics of the different grain sizes.

An examination of figure 2 will illustrate some of these characteristics:

1. The Wentworth grade classification of "fine sand" with an average diameter of .18 mm is the most easily moved, and the value of u_* necessary to cause initial movement and to cause roughness is numerically equal to the settling velocity. This indicates that grains of this size may be transported at relatively low velocities by surface creep, saltation and in suspension.

2. The threshold velocity for grain

sizes greater than .18 mm increases as the grain diameter increases. For these grain sizes the threshold velocity is greater than the roughness velocity and less than the settling velocity, indicating that the bottom is rough before movement takes place; and that when movement is initiated, it will be in the form of rolling and sliding rather than suspension.

3. The threshold velocity for grain diameters less than .18 mm increases with decreasing grain size. As previously mentioned this is probably due to the fact that the bottom is smooth and the drag is evenly distributed over the entire area rather than being applied to a few of the more exposed grains. Also, for these small grains the threshold velocity is much greater than the settling velocity. This indicates that if once put in suspension they will tend to be transported in suspension rather than by surface creep.

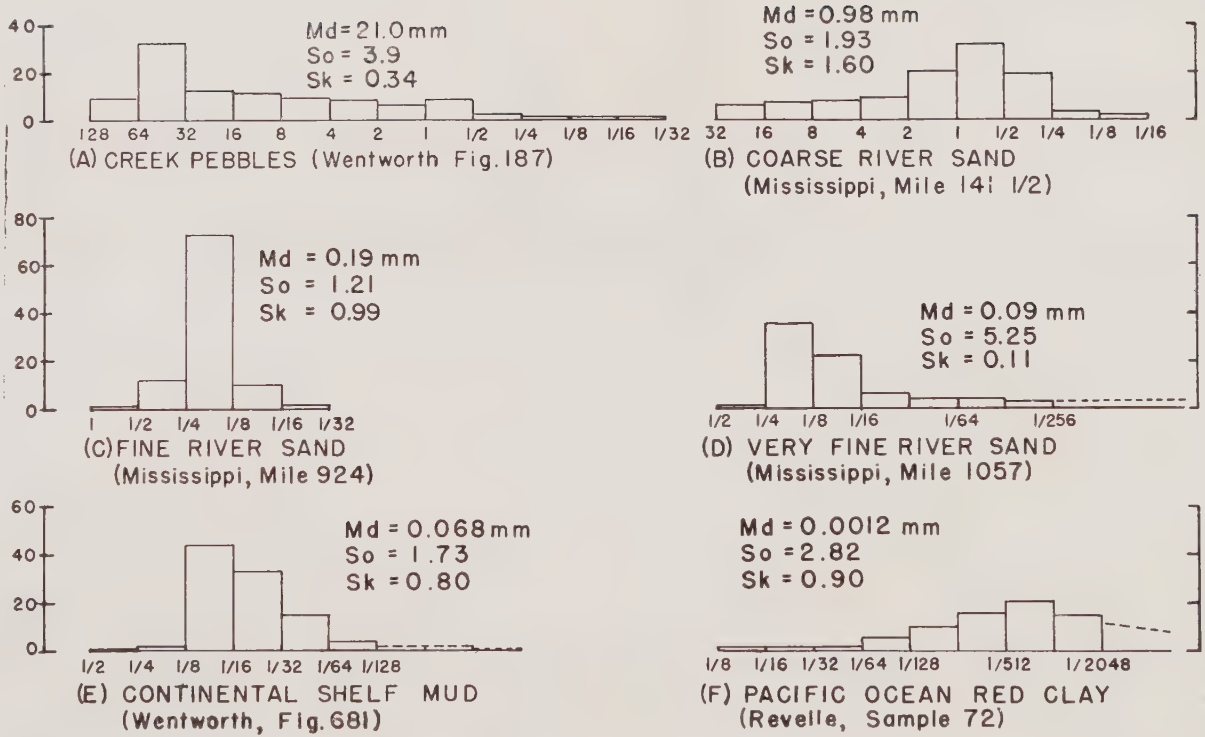
It is not clearly understood how material on a smooth bottom is put is suspension. Suspension over a hydrodynamically smooth bottom may be due to the presence of a lifting force as proposed by Jeffreys' (1929) and strengthened by White's (1940, p. 333) observations, or it may be due to increased bottom roughness by the formation of ripples after movement has beeen initiated.

Sorting: Russell (1939) divides sorting action into two types: "local" sorting involving the assortment of particles at a particular locality or site of deposition; and "progressive" sorting consisting of an assortment in the direction of transportation. Russell states: "The most important factors involved in both types of sorting appear to be the size, shape, and specific gravity of the particles, and the velocity, degree of turbulence, viscosity, and specific gravity of the transporting agent." It is also necessary to consider the methods of transportation and whether the sorting takes place during transportation or deposition or both. In this paper our discussion will be limited to spherical particles with a specific gravity near 2.65.

It would seem that the degree of sorting would be a function of the ability of the fluid to sort out one grain size from another. Grain sizes near .18 mm are hydrodynamically unique from all other sizes in that: (1) they are moved by weaker currents than grains smaller or larger than themselves; (2) once moved they do not have as great a tendency to go into suspension as do smaller grains; and (3) they are more readily carried into suspension than larger material. Thus where friction velocity does not greatly exceed the threshold velocity, fine sand marks the transition zone between transportation in suspension and transportation by surface creep. An inspection of figure 2 indicates that a current with a friction velocity that gradually decreases in the direction of transport will move bottom material near .18 mm a greater percentage of the time than any other diameter. Since both coarse and fine materials are more difficult to move and since very fine material is readily carried into suspension, bottom sediment in the process of transportation tends to become progressively better sorted as its median diameter nears .18 mm.

Sediments with median diameters either larger or smaller than .18 mm tend to be more poorly sorted; the tendency toward poor sorting being more pronounced for fine sediments. This may be accounted for by the fact that the fluid does not as readily differentiate between the smaller diameters. The fine sediments are more closely packed and the drag is evenly distributed over them. For a homogeneous size distribution the apparent threshold velocity increases with decreasing grain size below that of fine sand, however it seems probable that for an aggregate of fine sizes the threshold velocity is effectively constant for diameters less than .18 mm, so that different diameters of fine sediments will tend to move by surface creep as a group. Once in suspension, they will be completely removed to an area of much less current since the settling velocity is small compared with the threshold velocity.

In the absence of movement by surface creep, the great differences in settling



(A) CREEK PEBBLES (Wentworth Fig. 187)

(B) COARSE RIVER SAND (Mississippi, Mile 141 1/2)

(C) FINE RIVER SAND (Mississippi, Mile 924)

(D) VERY FINE RIVER SAND (Mississippi, Mile 1057)

(E) CONTINENTAL SHELF MUD (Wentworth, Fig. 681)

(F) PACIFIC OCEAN RED CLAY (Revelle, Sample 72)

Fig. 4.—Histograms of typical sediment types

(B), (C), and (D) are from the U. S. Waterways Experiment Station (1935); the numbers refer to miles below Cairo, Illinois.

velocities of very fine sediments act over large lateral distances as an effective sorting agent. For this reason very fine sediments, such as deep basin muds and clays derived only from the deposition of suspended material, may be better sorted than sediments with median diameters intermediate between them and fine sand.

Shallow Water Sediments Under Unidirectional Flow: Consider an hypothetical case in which the average velocity $\bar{u}$ and the random fluctuations u' near the bottom of a river or ocean current gradually decrease in magnitude in a downstream direction, and the initial upstream current causes a stress on the bottom sufficient to move all bottom material. Consider the supply of material to be continuous and to consist of all sediment grades from clays to cobbles. Under these flow conditions there will be a decrease in the threshold velocity in a downstream direction, and hence a gradual decrease in the median diameter[1] of the bottom samples. For a given size material this decrease in median diameter will depend upon whether the stream is in a condition of "degradation," "at grade," or "aggradation."

Consider the character of bottom samples obtained at various points downstream from the source material, when transported under the above flow conditions. Near its source where the stream is actively degrading its channel, the high values of friction velocity would cause the fine material including sand to be mostly in suspension. However, to maintain a suspended load, a portion of the fine material will be on the bottom. The bottom load at this point would consist predominantly of coarse material with decreasing amounts of fine. Since the sample is near the source and the friction velocity exceeds the threshold velocity for all but the coarsest material, it is to be expected that the sample will not be as well sorted as material farther downstream. Also, since it consists of coarse material with decreasing amounts of fine, the histogram of the sample will tend to be skewed toward the fine fractions. In other words, the median would be finer than the mode (see fig. 4a). It seems probable that the common finding of skewness values less than one in very coarse samples is due to a lag condition of this type.

Consider a bottom sample from a point farther downstream where the average friction velocity fluctuates between the threshold velocity for very coarse sand and granules (see fig. 2). Under these conditions it would seem that the bottom material transported by surface creep would consist predominantly of coarse and very coarse sand with decreasing amounts of granules and pebbles. There would also be finer grades present on the bottom, their amounts decreasing with decreasing diameter. This does not imply that the stream is transporting more coarse than fine material. The presence of coarse material would probably produce sufficient bottom turbulence to cause fine material to be placed in suspension. Since finer diameter materials have lower settling velocities, less material per unit area is required on the surface of the bottom to support a dense suspended load (see equation 13). It seems probable that medium sand would be transported both by saltation and in suspension; fine sand would be transported predominantly in suspension but partly by saltation; and very fine sand, silts and clays would be transported in suspension.

A bottom sample from the point where the friction velocity fluctuates between the threshold velocity for very coarse sand and granules would be better sorted than samples farther upstream because the flow characteristics of the stream that tend to sort material have acted over a greater time and distance. Also, the fine material is still largely transported in suspension, and the quantity of material transported by surface creep is inversely proportional to the particle diameter. These factors give a more homogeneous size distribution of bottom material (see fig. 4b).

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[1] The decrease in grain size due to abrasion may be an important factor, but due to the many variables it is not practical to consider here.

It might be expected that the histogram of this sample would be skewed toward the coarse grades, and consist predominantly of coarse and very coarse sand with decreasing amounts of granules and pebbles. However, Gilbert (1914), Chang (1939) and others have shown that once movement is initiated, larger particles tend to move faster and stop less frequently (due to greater momentum and the fact that their larger diameter places them in a faster field of flow) than finer particles. Mississippi River bottom samples collected by the U. S. Waterways Experiment Station (1935) indicate that samples with median diameters near 1.0 mm are predominantly skewed towards the coarse grades (fig. 4b), while those with median diameters between 1.0 and .18 mm are nearly symmetrical or have skewness values slightly less than one.

Next, consider a bottom sample from a downstream point where the average friction velocity fluctuates between the threshold velocity for fine and coarse sand. Bottom roughness would produce sufficient turbulence to cause suspension of fine material, including some fine sand. For reasons previously mentioned, the fine sand would be most easily moved; the coarser and finer grades moved by surface creep would tend to lag behind. For these reasons the bottom sample would have a median diameter near .18 mm, it would be well sorted, and have a symmetrical size distribution (fig. 4c).

As a final hypothetical case, consider the character of a bottom sample still farther downstream from the above points where the stream has a friction velocity near, but not execeding, the threshold velocity of fine sand. Therefore, material coarser than fine sand would be almost entirely absent. The bottom material transported by surface creep would consist predominantly of fine sand with decreasing amounts of finer material The presence of fine sand would produce sufficient bottom turbulence to cause finer material to be in suspenion. However, the decrease in friction velocity would require a large percentage of fine material per unit area on the surface of the bottom to maintain a suspended load. Thus the bottom sample would consist mainly of fine sand with gradually decreasing amounts of finer material. The sample would have a median diameter less than .18 mm, it would not be as well sorted as slightly coarser material, and the histogram of the sample should show a pronounced skewness toward the fine fractions (fig. 4d).

Sediments found under flow conditions similar to those postulated above are in agreement with the hypothetical bottom samples. This agreement is strengthened by an inspection of the 615 Mississippi River bottom samples collected from Cairo, Illinois, to the mouth of the river by the U. S. Waterways Experiment Station (1935). Since the U. S. Waterways' samples ranged in location from mid-channel to bars, and were often influenced by sediments from tributary streams, it is to be expected that individual samples will vary widely in character. However, their general tendencies are significant. The sediments have a sorting coefficient near 3 just below Cairo Illinois, where the median diameter falls in the coarse sand grade. The median diameter decreases downstream and the sorting improves. A sorting of 1.2 is obtained above New Orleans where the median diameter is .18 mm. Below this point the sorting coefficient has a value greater than 5 for bottom samples with median diameters near .09 mm. The bottom samples near Cairo are predominantly skewed toward the coarse grades. The symmetry of the sample improves in a downstream direction. Near New Orleans where the median diameter is .18 mm, the samples have a symmetrical size distribution. As the median diameter becomes finer below New Orleans, the histogram of the bottom samples show a marked skewness toward the fine grades. A graphic representation of the distribution of sediment sizes in the Mississippi River samples, averaged by 25 mile intervals, is shown in figure 5.

A preliminary examination of that portion of the 828 typical sediment samples collected by Wentworth (1932) that relate to the present discussion show that samples having median diameters near .18 mm are predominantly well sorted and symmetrical. Samples having median diameters less than .18 mm are predominantly poorly sorted and skewed toward the fine grains. The coarser median diameter samples are more poorly sorted than fine sand samples and are skewed toward both the coarse and the fine. Coarse sand and granules from rivers and creeks were predominantly skewed toward the coarse grades. Pebbles and gravels from rivers and creeks were predominantly skewed toward the fine grades.

Sediments Derived from Suspension: In discussing fine sediments it should be noted that the colloidal fractions (less than 1 micron) of a sample are not necessarily subject to the hydrodynamic relations discussed in this paper. Furthermore, Gripenberg (1934) and Rouse (1939) point out that material less than 15 microns in diameter will often flocculate, and that mechanical analysis of deflocculated samples may yield histograms which bear little relation to the actual material in suspension.

Rouse (1939), in an analysis of the effect of turbulence on transportation of sediments in suspension, showed that with increasing height above the bottom, the sediment in suspension becomes more poorly sorted and its median diameter becomes finer. From these observations and the fact that bottom-transported fine sediments are predominantly skewed toward the fine, one would expect that pelagic sediments derived only from suspension (i.e., deep basin sediments) would tend to be nearly symmetrical or skewed slightly toward the coarser grades. As mentioned under sorting, very fine sediments may be better sorted than sediments with median diameters intermediate between them and fine sand. This ideal sample is frequently complicated in nature by the settling of organic material (calcareous and siliceous ooze) from the euphotic zone. Organic samples of this type are not subject to the same conditions as the inorganic since they have travelled relatively short horizontal distances. The fact that they are not subjected to the same transportation conditions is illustrated by the frequent double maxima in deep sea sediments. Revelle (1944) showed that double maxima were frequently due to organic material.

Deep basin mud and clay samples were obtained in the Pacific by the Carnegie Expedition (Revelle, 1944) and in the North Atlantic by the Meteor Expedition (Correns, 1939). Neglecting samples with double maxima, these deep sea sediments are characterized by a medium degree of sorting, and in general are either skewed toward the coarse grade sizes or have skewness values near one (figure 4f). Gripenberg (1934, p. 203) discusses some of the factors influencing the size distributions of bottom samples from the North Baltic Sea. Many of the histograms of her samples are skewed toward the coarse grades.

Beach Sediments: It is well known that beach sands are among the best sorted sediments. They are subjected to a progressive sorting when transported by longshore currents, and to a very effective local sorting by the oscillatory motion of the waves. Observations of southern California beach sands indicate that their sorting coefficients bear the same general relationship to median diameter as sediments from other environments, the difference being mainly in the degree of sorting (fig. 1).

Grant (1943) points out that theoretical studies and observations of oscillatory wave phenomena prove the existence of a shoreward mass transport of water, and that there is evidence of a differential in the velocity of the offshore and onshore orbital movement in the surf zone. LaFond (1939) shows that a

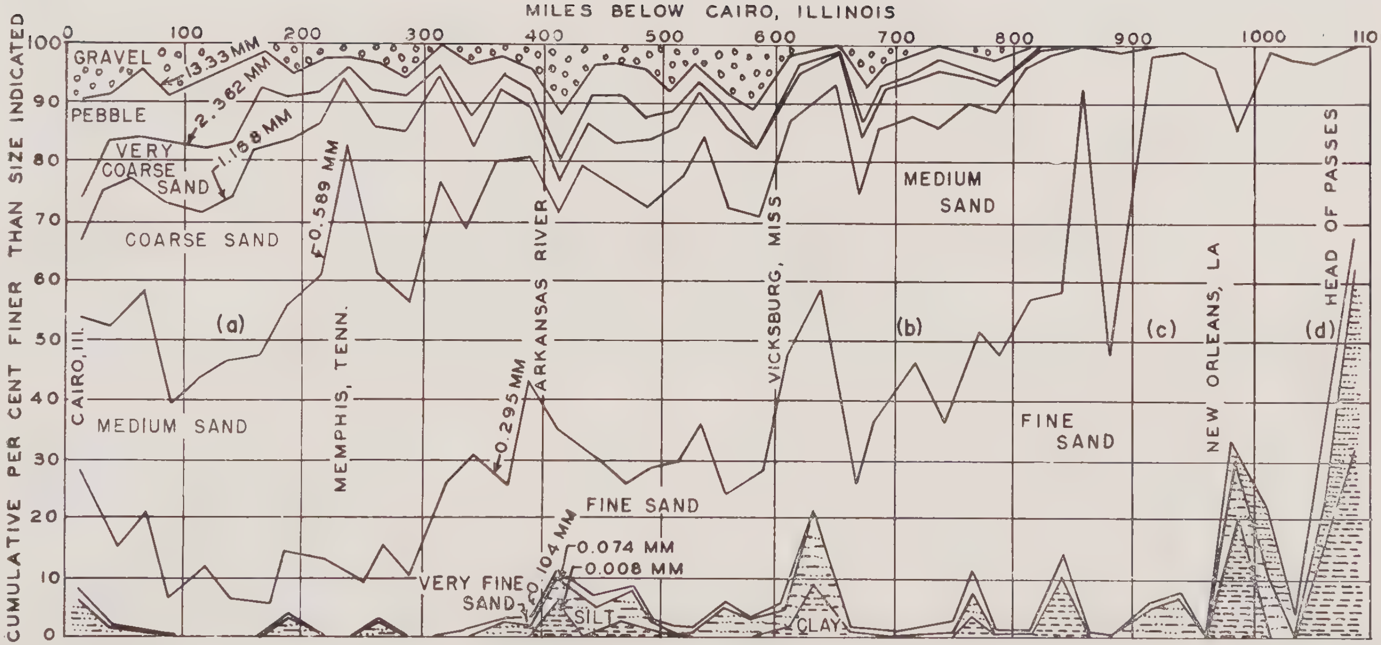

FIG. 5. Variation in composition of Mississippi river bed materials (from the U. S. Waterways Eoperiment Station, 1935). Statistical parameters of samples at localities indicated by letters are:

	Md(mm)	*So*	*Sk*
(a)	0.98	1.93	1.60
(b)	0.42	1.41	1.18
(c)	0.19	1.21	0.99
(d)	0.09	5.25	0.11

direct relationship exists between the fluctuations in the amount of sand on the beaches and the variations in wave size and type.

The orbital or particle motion associted with shallow water surface waves, relative to a fixed point, is thought to consist of a slow seaward velocity under the wave trough, followed by a rapid shoreward surge as the crest passes over the point. Adaptation of the solitary wave theory to the surf zone (Munk, 1949) gives quantitative values to these relationships and, if valid, indicates that the differential between the crest and trough velocities decreases as the wave height and frequency increase.

The shoreward mass transport of water apparently causes a rise in the sea surface near shore. This "piling up" of water must be compensated by a seaward return, part of which is known to be in the form of rip currents (Shepard, *et al.*, 1941). The solitary wave theory requires that the shoreward mass transport attain a maximum at the water surface and decrease with depth. Munk suggests that, in addition to rip currents, this transport is compensated by a uniform seaward return flow. This would result in a net shoreward drift near the water surface and a net seaward drift near the bottom.[1] The intensity of the seaward drift along the bottom would be a function of wave height and period, and may be negligible for low amplitude long period waves.

If one assumes that all these facts are valid when applied to the sorting of beach sediments, it would appear that sands, and particularly fine sands, would be the most transient beach material. Under waves of medium intensity, fine sand would be moved by both crest and trough orbital velocities, thus tending to give fine sand a zero net transport. Under the same conditions coarse material would be moved only by the rapid surge associated with the wave crest, and hence would move shoreward. Fine material would have a greater tendency to be in suspension and would be transported seaward by rip currents and any net bottom drift.

Under less intense wave conditions, sand size material would have a net shoreward transport where as very fine material would still have a tendency to be transported seaward.

Under conditions of high amplitude short period waves, sand size material would be transported both by crest and trough velocities. However, the increased friction velocity would cause sand size material to be in suspension, and thus have a net seaward transport. This analysis is an amplification of suggestions made by Grant (1943) and by Munk (1949). It should be noted that there will always be a size material for which the net transport will be zero, and if such material is available, it will become the predominant foreshore beach material. It will be locally well sorted, since finer material will be transported seaward and slightly coarser material will be deposited on the beach. The presence of cobbles at the base of most sand beaches may be attributed to the fact that the largest material moved will be transported shoreward.

CONCLUSIONS

The general relationship of sorting coefficient to median diameter appears to be similar for all water environments, the difference being mainly in the degree of sorting. Sediments with median diameters near the grade of fine sand are the best sorted; sediments coarser and finer are more poorly sorted.

The relationship of skewness to median diameter is more complex (fig. 1). Inspection of Mississippi River bottom samples from a point well above Cairo to the mouth of the river indicate that plots of skewness coefficient against median diameter go through several cycles (fig. 4).

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[1] If such a drift exists, its magnitude does not exceed a few centimeters per second, and thus should not be referred to as "undertow." Computations based on the solitary wave theory (Munk, 1948) indicate that a 4 foot high, 8 second period wave in water 15 feet deep would have a 119 cm/sec. orbital crest velocity, a 67 cm/sec. orbital trough velocity (seaward), and a net seaward bottom drift of 1.5 cm/sec.

The relationship of settling velocity, threshold velocity and roughness velocity to the diameter of the grain size (fig. 2) may serve to explain some of the observed correlations between sorting, skewness and median diameters in actual sediment samples. The curves in figure 2 are supported by theory and experimental observations. However, it should be remembered that the hypothetical examples given above were limited in scope and were discussed for rigidly controlled conditions. In nature the amount and type of sediment source, the degree of turbulence and the magnitude of the currents and their fluctuations, the distance the material has been transported, reduction of grain size by abrasion, and the time intervals involved, are all variables that must be considered.

Krumbein (1939) illustrates with isopleth maps of the sediment parameters of Barataria Bay "that the characteristics of the sediments reflect the general conditions of their formation. . . ." It is hoped that in the future more detailed analysis of the interrelationship of the statistical sedimentary parameters, sorting, skewness and median diameter, to the hydrodynamic conditions of transportation will be made, so that these sedimentary parameters will become a more definite clue to the processes under which the sediment was transported and deposited.

NOTATION AND DIMENSIONS

(All units are in the c.g.s. system; M is mass in grams, L is length in centimeters, T is time in seconds.)

Symbol	*Description*	*Dimension*
a	Reference level used in equations 12, 13 and 14	L
A	Eddy viscosity	$ML^{-1}T^{-1}$
B	Projected area of a particle in the direction of motion	L^2
c	Settling velocity	LT^{-1}
C_D	Drag coefficient	Dimensionless
d	Particle diameter; centimeters for all equations, millimeters for graphs	L
e	Base of natural logarithms	Dimensionless
f_c	Critical tractive force on a spherical particle	MLT^{-2}
F_D	Frictional drag force on a moving particle	MLT^{-2}
g	Acceleration due to gravity	LT^{-2}
i	Slope; value in radians of the angle between the water surface and a horizontal plane	Dimensionless
k_0	von Kármán's flow constant, equals approximately 0.4	Dimensionless
l	Prandtl's mixing length	L
ln	Natural logarithm	
Md	Geometric median diameter; millimeters	L
n	Positive number equal to u_*/c	Dimensionless
p	Packing coefficient	Dimensionless
Q_1, Q_3	First and third quartile measures; millimeters	L
R	Reynolds number; $\frac{vd}{\nu}$	Dimensionless
S	Concentration of suspended particles expressed as mass per unit volume of water	ML^{-3}
Sk	Skewness coefficient; $\frac{Q_1Q_3}{Md^2}$	Dimensionless
So	Sorting coefficient; $\sqrt{\frac{Q_1}{Q_3}}$	Dimensionless
u	Instantaneous velocity in the x-direction; positive downstream	LT^{-1}

$\bar{u}$	Mean downstream velocity	LT^{-1}
u'	Velocity of random fluctuation related to turbulence in a downstream direction	LT^{-1}
u_*	Friction velocity; $\sqrt{\frac{\tau}{\rho}}$ u_{*c} is the threshold velocity necessary to move a given size particle u_{*r} is the roughness velocity	LT^{-1}
v	Velocity of a particle relative to the fluid	LT^{-1}
w'	Random fluctuation related to turbulence in the z-direction; positive upward	LT^{-1}
x	Horizontal axis; positive downstream	L
z	Vertical axis; positive upward	L
z_0	Roughness length, related to the height of the roughness elements	L
α	Factor depending upon the type of flow	Dimensionless
γ	Factor depending upon the height at which $\bar{u}$ is measured above the bottom and the degree of bottom roughness; γ^2 is commonly referred to as the resistance coefficient (Munk, 1948)	Dimensionless
δ	Thickness of the laminar boundary layer	L
λ	Flow constant (usually defined as $\lambda + \frac{1}{k_0} \ln k_0 = 5.5$)	Dimensionless
μ	Molecular viscosity	$ML^{-1}T^{-1}$
ν	Kinematic viscosity; μ/ρ	L^2T^{-1}
ρ	Mass density of the fluid	ML^{-3}
ρ'	Difference between mass density of the particle and that of the fluid	ML^{-3}
τ	Intensity of fluid shear per unit area; tractive force per unit area	$ML^{-1}T^{-2}$
τ_c	Critical tractive force per unit area exerted on the surface of the bottom by the fluid	$ML^{-1}T^{-2}$
ϕ	Angle of repose (degrees)	Dimensionless

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THE ENERGY ACQUIRED BY THE ATMOSPHERE OVER THE OCEANS THROUGH CONDENSATION AND THROUGH HEATING FROM THE SEA SURFACE

By Woodrow C. Jacobs

THE ENERGY ACQUIRED BY THE ATMOSPHERE OVER THE OCEANS THROUGH CONDENSATION AND THROUGH HEATING FROM THE SEA SURFACE

By Woodrow C. Jacobs[1]

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(Manuscript received 17 January 1949)

ABSTRACT

Making use of previously derived seasonal and annual values of sensible heat exchange and precipitation for the oceans, charts have been prepared which show the total energy acquired by the atmosphere over the North Atlantic and North Pacific through the conduction of sensible heat from the sea surface and through the condensation of water vapor.

The winter values for the total energy have been compared with Wexler's (1944) values for the total heat acquired by the atmosphere within the layer from the surface to 3 km over the northern hemisphere during February. An excellent agreement is found between the two sets of values within the western Atlantic area. However, a difference chart of the two sets of data indicates that Wexler obtains higher values in the far western and southeastern portions of the oceans but lower values over the central and northeastern portions of the oceans. An analysis of the problem leads to the conclusion that the two quantities arrived at by different methods should agree only in the absence of mean vertical motion within the atmosphere. In the presence of mean vertical motion it is reasoned that the two sets of data will differ, the sign of the difference depending upon whether there is divergence or convergence within the 3-km layer over the region, and the magnitude of the difference depending upon the net amount of convergence or divergence.

1. Introduction

In previous papers (Jacobs, 1942; 1943) the writer has presented data on the rate of total energy exchange ($Q_a = Q_c + Q_e$)[3] between sea and atmosphere over the North Atlantic and North Pacific. Up to this point, the computations have given the rate of total energy loss (or gain) from the sea surface by conduction to the atmosphere. From the standpoint of the sea surface, this exchange is entirely in the form of sensible heat. In the case of the atmosphere, on the other hand, only that portion of the energy given off directly as sensible heat (Q_c) is immediately available for heating the air. The remaining energy (Q_e) is in the latent form of water vapor. In order to obtain a picture of the seasonal and regional distribution of the areas of heating and cooling in the atmosphere comparable to the picture obtained for the ocean surfaces by the plotting of the Q_a values, it is necessary to examine the seasonal and regional variations in the amount of sensible heat made available to the atmosphere through the liberation of the latent energy of the water vapor by condensation.

In the earlier investigation on the energy exchange between sea and atmosphere, the writer regarded heat transfer by conduction across the ocean surface (Q_c) and heat transfer by evaporation or condensation (Q_e) as two physical entities, the rate of heat loss (or gain) from the ocean being obtained by adding these two quantities. Montgomery (1948) has recently evolved a direct method for estimating the total eddy flux of heat from a water surface by combining the effects of heat transfer by conduction and heat transfer by evaporation or condensation.

It is true that Montgomery's equations will facilitate the computations of the rate of total heat loss from the sea surface (Q_a) and their use should serve the requirements of the oceanographers except, perhaps, to the extent that the latter group is interested in the water budget of the oceans, the effects of evaporation on surface salinities, *et hoc*. The meteorologist, however, is interested in the separate fractions of the energy exchange, Q_c and Q_e, and in the water vapor made available to the atmosphere through evaporation from the sea surface. The first quantity represents energy which is locally available for heating the atmosphere; the second quantity represents potential energy which is not realized as heat until condensation takes place. Moreover, any meteorological investigation which involves consideration of air-mass transformation should concern itself with the exchange of moisture as well as the exchange of sensible heat.

2. Method of computation

A consideration of the problem leads to the conclusion that the amount of energy released to the atmosphere through the condensation of water vapor can be obtained, completely, from data concerning precipitation amounts over the oceans. While it is true that the latent energy of the water vapor is released at the time of condensation in the form of cloud, it is only that portion which falls out as precipitation which contributes its latent heat permanently to the atmosphere. A cloud which forms and subsequently dissipates has contributed zero energy because the same amount of energy is used to evaporate the cloud as was released through its formation. The same reasoning applies to the evaporation from the raindrop or snow crystal. In this case the energy for the evaporation is also supplied by the atmosphere; therefore, it is only that portion of the precipitation which actually falls to the sea surface which needs to be considered.

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[2] Contribution from the University of California, Scripps Institution of Oceanography, New Series, No. 428.

[3] A table of symbols and constants is given at the end of this article.

The fraction of energy which is released to the ocean by the direct condensation of water vapor upon the sea surface, when the vapor pressure increases upward from the sea surface, has already been considered by the writer in a previous paper (Jacobs, 1942), and the amounts are subtracted in the computations for Q_a.

The only possible correction that might be applied is one due to a fraction of the amount of energy represented by the cloud amount when the *mean* cloudiness differs between one season and the next. However, since the energy which it would be necessary to add (or subtract) for the *entire season* is equal only to the energy represented by the *difference* between the *average* amount of liquid water in cloud form during one season and that quantity for the next season, simple computations would show that this correction is completely insignificant.

The sensible heat equivalent (cal cm^{-2} per unit time) of the precipitated water is given by:

$$Q_p = L_t P, \qquad (1)$$

where L_t is the latent heat of condensation at the condensation temperature, t. It was originally assumed that a reasonable average condensation temperature for the atmosphere over the oceans would be 0C. However, this latter temperature gives a value for L_t of 595 cal g^{-1}. (Refer to formula for L_t given in the table of symbols.) It will be recalled that, when considering Q_e (Jacobs, 1942), L_t was taken as 585 cal g^{-1}, representing a reasonable average value for the observed sea-surface temperatures. The difference of 10 cal g^{-1} between the accepted value for the latent heat of evaporation and the proper mean value for the latent heat of condensation leads to the anomalous result that the energy acquired by the atmosphere exceeds that which is given up by the sea surface—an apparent violation of the principle of conservation of energy. This difference is due to the change of latent heat of vaporization with temperature which, according to Holmboe *et al.* (1945), is given by:

$$dL_t/dT = c_{pv} - c_w,$$

where c_{pv} is the specific heat of water vapor at constant pressure, and c_w is the specific heat of liquid water. This apparent error has been circumvented by assuming that the temperature of condensation is equal to the temperature of evaporation, and thus assigning a value of 585 cal g^{-1} for L_t. However, the difference between the two values is small enough (less than 2 per cent) to be considered completely insignificant.

One source of error, which may be important locally during the winter season, is introduced through the assumption in (1) that all precipitation is in the form of liquid water. While this is generally true for most of the ocean areas considered, there are small portions of each ocean at the higher latitudes where at least some of the precipitation is in the form of snow during the winter season. When dealing with precipitation entirely in the form of "dry" snow or other ice products (such as sleet,[4] *etc.*), equation (1) takes the form:

$$Q_p = L_{iv} P, \qquad (2)$$

where P, in this case, is the "water equivalent" of the melted snow (or sleet) and L_{iv} is the latent heat of sublimation of water vapor. ($L_{iv} = L_t + L_i$, where L_t is again the latent heat of condensation of water vapor and L_i is the latent heat of fusion of liquid water.) Since $L_i = 80$ cal g^{-1},

$$L_{iv} = 675 \text{ cal g}^{-1}$$

when L_t is taken to be equal to 595 cal g^{-1}.

Thus an error is introduced into the computations when considering the total energy made available to the atmosphere (in this case through the sublimation of the water vapor), because the heat required for melting the snow which falls to the sea surface is supplied by the sea and not by the atmosphere. However, even if it is assumed that *all* precipitation at the higher latitudes occurs in the form of unmelted snow, the total error cannot exceed about 12 per cent. In actuality, only a fraction of the total precipitation will occur as snow, so the probable error is much less. In any event, the error could be significant only at the higher latitudes and only during the winter season.

The same reasoning applies to precipitation in the form of hail. However, hail is of rare occurrence over the oceans and can be neglected.

Since the values for precipitation over the oceans have been given (see section 3) in cm per season (equivalent to g cm^{-2} per season) and it was desired to have the energy equivalent Q_p given in cal cm^{-2} day^{-1}, for purposes of convenience equation (1) has

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[4] Sleet is given the usual U. S. interpretation "grains of ice" rather than the English interpretation "snow and rain occurring together."

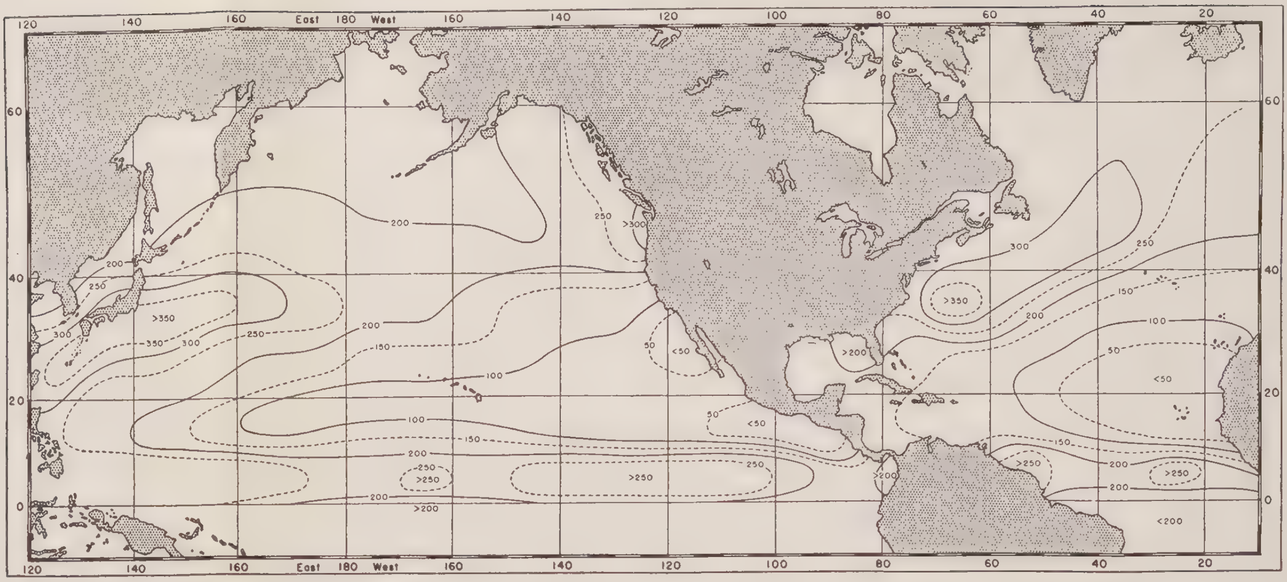

FIG. 1. Mean values of the rate at which total energy is made available to the atmosphere (Q_{pc}) through the exchange of sensible heat with the sea surface (Q_c) and through the condensation and precipitation of water vapor (Q_p) during winter (December, January, February) expressed in cal cm^{-2} day^{-1}.

been put in the form:

$$Q_p = n^{-1} L_t P_s, \tag{3}$$

where n is the number of days in the season.

When n is 91 and L_t is 585 cal g^{-1}, (3) becomes:

$$Q_p = 6.43 P_s \text{ cal cm}^{-2} \text{ day}^{-1}. \tag{4}$$

This latter form has been used throughout the computations except for the adjustments required by the different values for n.

3. Source of precipitation data

Before computations of the energy of condensation could be obtained through the use of formula (3), it was necessary to obtain reasonably correct data concerning seasonal and annual precipitation amounts over the oceans. However, an examination of the extensive literature on the subject of distribution of precipitation indicated that not only have there existed no seasonal data on precipitation amounts over the oceans, but that the few data on the annual amounts have been subject to criticism. In order to obtain approximately correct annual precipitation values over the oceans, the published regional data were brought into agreement with Wüst's (1936) more reliable zonal values by the assignment of simple correction factors for each of the oceans. Upon this basis, a new chart of the annual precipitation over all oceans was prepared.

Then, through the use of published climatological data on the seasonal frequencies of precipitation over all oceans (U. S. Weather Bureau, 1938), seasonal precipitation charts were prepared.

In an as yet unpublished paper,[5] the writer has shown that approximately correct values of the relative seasonal amounts of precipitation for each 10-degree square over the oceans can be obtained through the use of the expression

$$P_s = F_p P_a \div \sum_{i=1}^{4} F_{pi} \tag{5}$$

where P_s is the seasonal precipitation rate (g cm^{-2} season^{-1}), P_a is the annual precipitation and F_p is the seasonal frequency of Greenwich meridian noon observations showing precipitation of any type. The complete series of seasonal precipitation charts is contained in the unpublished manuscript referred to above.

4. Results of the computations

On the basis of formula (3) and the precipitation data just described, computations of the seasonal and annual values of Q_p have been made for each 10-degree square over the oceans. The results are not reproduced here, because it is obvious that the seasonal and annual charts of Q_p for the oceans are identical in configuration to the precipitation charts upon which they are based. Of greater interest are the charts showing the rate at which total energy is acquired by the atmosphere, both through the condensation of water vapor and through the exchange of sensible heat with the sea surface. The sensible heat quantities, Q_c, are given in a previous publication (Jacobs, 1943). The total energy, Q_{pc}, is obviously the sum of the two quan-

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[5] W. C. Jacobs, "The energy exchange between sea and atmosphere and some of its consequences," (to be published as a technical monograph of the Scripps Institution of Oceanography).

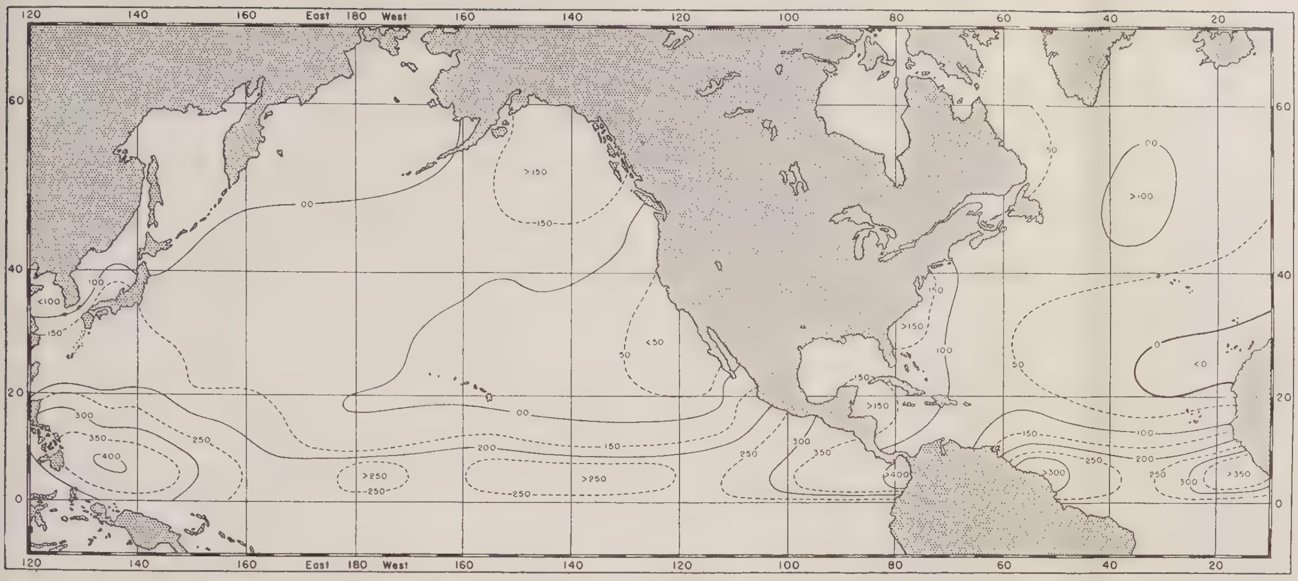

Fig. 2. Mean values of the rate at which total energy is made available to the atmosphere (Q_{pc}) through the exchange of sensible heat with the sea surface (Q_c) and through the condensation and precipitation of water vapor (Q_p) during summer (June, July, August) expressed in cal cm^{-2} day^{-1}.

tities, *i.e.*:

$$Q_{pc} = Q_p + Q_c \text{ (cal cm}^{-2}\text{ day}^{-1}). \qquad (6)$$

The results of the computations for the summer and winter seasons only are given in figs. 1 and 2.

The configuration of the isopleths on the Q_{pc} charts is quite different from that on the Q_a charts, as is to be expected. The subtropical areas of maximum rate of energy exchange which appear on the Q_a charts are conspicuously absent, being replaced by a long belt of minimum values on the Q_{pc} charts. These values are highest along the Equator, along the western sides of the oceans and, in the North Pacific, along the extreme northeastern coast. The regions of lowest energy are, in both oceans, centered along the eastern coasts in the subtropical latitudes. The maxima which appear along the western coasts at midlatitudes are most pronounced during the winter season, as would be expected, since that is the season which presents very large values for Q_c over these portions of the oceans.

As shown by fig. 3, the latitudinal values for Q_{pc} show decided minima in the subtropical latitudes, with the principal maxima in the equatorial regions. However, the winter values at high latitudes are of the same order of magnitude as the equatorial values. At the lower latitudes the maximum values occur during summer, the minimum values in spring. At higher latitudes, on the other hand, the maximum values occur during winter, and the minima during summer.

It thus appears that the principal sources of heat energy for maintaining the general circulation over the oceans are in the equatorial regions and at the higher latitudes. The subtropical latitudes appear as regions where very little heat energy is being supplied to the atmosphere. Because it is obvious that the surface layers of the atmosphere are not undergoing cooling in these latitudes, the latter situation suggests that the trade-wind areas of both oceans must be

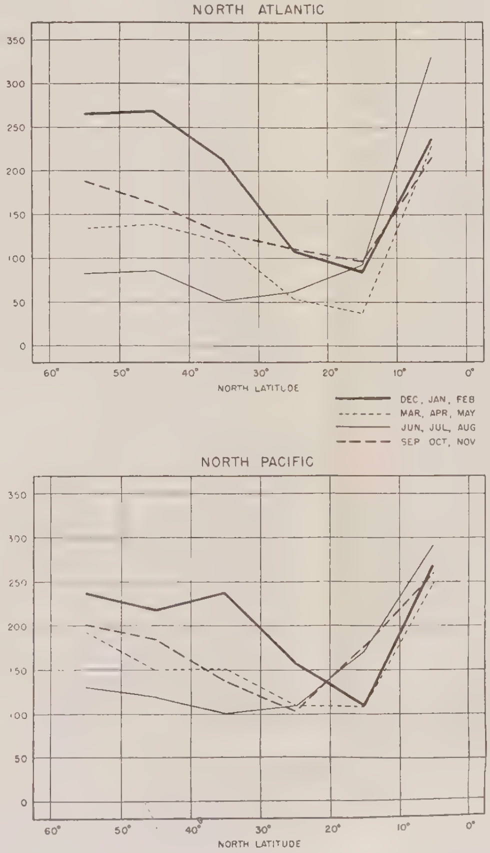

Fig. 3. Seasonal values of Q_{pc} over the North Atlantic and North Pacific arranged by latitude. The ordinate is Q_{pc} in cal cm^{-2} day^{-1}.

regions where significant amounts of kinetic and gravitational potential energy are being converted into heat, at least within the lower atmospheric layers. The very large rate of transfer of energy in these regions which is indicated on the Q_a charts does not make itself felt until it is released in the zone of the equatorial convergence (or along the polar front at higher latitudes).

The principal sources of heat energy for maintaining the circulation at the higher latitudes are probably the western portions of the oceans (particularly in winter) and the central and eastern portions of the oceans, poleward from latitude 40°N.

5. Comparison of the results with Wexler's values of layer heating

Wexler (1944), by another method, has computed the amount of heat acquired during February by the atmospheric layer between sea level and 10,000 feet. His computations cover the North Pacific, North Atlantic, and North America between approximately the 20th and 60th parallels. His method has been to examine the mean transport across the normal mean isotherms of the 3-km layer, assuming that the normal mean isotherms are stationary.

He has previously compared his results with the writer's winter values for Q_c and finds a good qualitative agreement. However, as shown by fig. 4, in regions of marked layer heating his values lie intermediate between the values for Q_c and Q_a, indicating a greater amount of layer heating than can be accounted for by the conduction of sensible heat from the sea surface but a lesser heating than would be required if the total latent energy supplied to the atmosphere through evaporation were locally realized as sensible heat. When his values are compared with the Q_{pc} values averaged for the same areas, however, an almost perfect agreement is shown (fig. 4).[6]

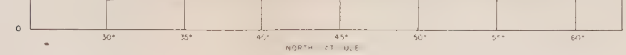

FIG. 4. Comparisons between the average latitudinal values for Q_c (curve B), Q_a (curve C), Q_{pc} (curve D) and Wexler's values for the total heating of the atmosphere between the surface and 10,000 feet (curve A). The values have been computed, in all cases, for the western North Atlantic between the coast and the region where Wexler's values reach zero (approximately in mid-ocean). The ordinate is labelled in cal cm^{-2} day^{-1}.

Nevertheless, a comparison between Wexler's chart and the chart which presents the winter values for Q_{pc} (fig. 1) shows that regional differences between the two do exist. A consideration of the problem indicates that the two sets of values should agree only in the absence of *net* vertical motion within the 3-km layer and only if the effects of the radiative flux of heat can be neglected. While the data are insufficient to allow a rigorous theoretical treatment of the problem, a qualitative analysis of the results is permitted.

It is reasoned that, in regions which show net horizontal velocity convergence below the 3-km level, the layer heating will be less than that indicated by the Q_{pc} charts due to the transport of energy into the atmospheric layers above 3 km. On the other hand, regions which show net horizontal divergence below the 3-km level will exhibit a layer heating greater than that indicated by the Q_{pc} charts, due to the effects of transport of energy downward (subsidence) from higher levels. The mechanism for the vertical exchange of energy would thus appear to be supplied by the regional differences in Q_{pc}, while the mechanism for the lateral exchange of energy would appear to be supplied by the observed upper-level circulations.

The layers above 3 km over the regions of horizontal convergence acquire energy through vertical heat transport and, at the same time, gain in gravitational potential energy through vertical mass transport. Part of the heat thus acquired is lost through radiative processes, but part is retained to maintain an increased potential temperature in the upper layer. On the other hand, the upper layers above the regions where there is net horizontal divergence may receive energy through horizontal transport but must lose gravitational potential energy through vertical mass transport (subsidence). The lower divergent layer will thus acquire, as sensible heat, the portion of Q_{pc} which exceeds that lost through radiative processes in the upper atmosphere.

Neglecting the effects of radiative flux of energy, the difference between Wexler's values and the Q_{pc} values should then constitute a quantitative measure of horizontal convergence and divergence within the 3-km layer. The sign of the difference should indicate whether there is net convergence or divergence, while the magnitude of the difference should indicate the net amount of convergence or divergence. However, since radiative processes can probably not be neglected, it does not appear profitable at this time to subject the data to quantitative treatment.

A qualitative difference chart between the two sets

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[6] All values given in fig. 4 are averages for the region in the North Atlantic between the North American coast and a line, approximately in mid-ocean, where Wexler's values reach zero.

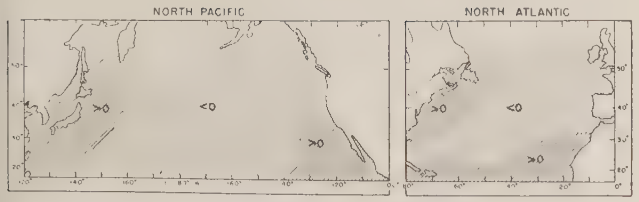

FIG. 5. A difference chart between Wexler's (February) values for the total heating of the atmospheric layer between the surface and 3 km and the winter values for Q_{pc}. The regions where the difference ($Q_{\text{Wexler}} - Q_{pc}$) is positive are assumed to be regions of net divergence within the 3-km layer, while the regions where the difference is negative are assumed to be regions where there is net convergence within the layer.

of data, which is given as fig. 5, shows regions of net divergence ($Q_{\text{Wexler}} - Q_{pc} > 0$) in the western and southeastern portions of both oceans and regions of net convergence ($Q_{\text{Wexler}} - Q_{pc} < 0$) in the central and northeastern portions. The areas of divergence in the southeastern portions of both oceans would probably appear greater in extent had it been possible to extend the computations southward beyond 20°N (which is the southerly limit of Wexler's data). The equatorial regions, however, would undoubtedly appear as areas of convergence.

The centers of Wexler's areas of maximum heating are located over the oceans near the eastern coasts of the two continents and coincide with the winter areas of maximum Q_{pc}. Fig. 5 shows, however, that the regions of maximum divergence are probably centered over the continents at some distance westward from the coast. This would indicate that the eastern portions of the continents at midlatitudes (and perhaps the arctic, also) are regions of divergence during this season. The secondary areas of maximum heating in the southeastern portions of the oceans shown by Wexler's chart do not coincide with any regions of maximum Q_{pc}. It must therefore be concluded that the heating in these areas is primarily due to subsidence. Similar lines of reasoning indicate that regions of convergence are centered over the western portions of the continents at the higher latitudes.

In the absence of radiative loss of heat, a complete difference chart for the northern hemisphere (including the land surfaces) would show approximately equal amounts of convergence and divergence. However, since the radiative loss of heat by the upper layers does occur, the method of computation would require that the energy equivalent of the total convergence exceed that of the total divergence by an amount equal to the excess radiative loss of energy. However, energy exchange values for land surfaces, equivalent to the Q_{pc} values for the oceans, are not available for testing the above hypothesis.

Elliott and Smith (1949), have discussed the significance of the differences between the author's Q_a values and Wexler's data, stressing the importance of "lateral turbulence" processes in transferring energy from the principal *sea-surface* energy sources off the east coasts of the continents to the regions of the Aleutian and Icelandic lows. They have reasoned that the latent heat supplied to the atmosphere off the east coasts (in winter) is released as real heat primarily in the latter two areas. A comparison of the Q_a charts (Jacobs, 1942) and the present Q_{pc} charts lends support to this concept and is in line with the conclusions drawn in section 4. They also stress again the importance of taking into account anomalies in the energy loss from the ocean surfaces off the east coasts when considering "long-period anomalous behavior in circulation patterns" over the northern hemisphere.

6. Remarks on radiation effects

The quantity Q_{pc} presented in the last section represents the total amount of energy made available to the atmosphere through convective processes over the oceans. The quantity does not include the amount of energy the moist atmosphere receives by the absorption of long-wave terrestrial radiation nor the small absorption of direct solar energy. In regions where the atmosphere is at a much lower temperature than the underlying sea surface, the Q_{pc} values will be too small to accurately represent the total heating of the atmospheric layer. In regions where the sea surface is at a much lower temperature than the overlying air mass, the Q_{pc} values will be too large by the excess amount of energy which the moist atmosphere radiates to the sea surface.[7] The end result, of course, is that the total energy acquired by the atmosphere through the absorption of radiant energy and through convective processes must exactly balance the radiative loss. A complete analysis of the energy balance within the atmosphere over the oceans, then, requires a consideration of the radiative as well as the convective transfer of energy. The analysis of the radiative effects, however, is beyond the limits set for the present investigation.

7. Remarks on the buoyancy effect of water vapor

One possible source of convective energy over the oceans which has not been mentioned up to this point is that due to the Archimidean forces produced in the lower layers of the atmosphere by the addition of water vapor (through evaporation from the sea surface). This "partial" convective factor has been referred to as "water convection."[8] However, simple computations show that the total effect is small and probably limited to the layers below 1 km and that it can be neglected, at least as far as its influence on the general circulation of the atmosphere over the oceans is concerned.

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[7] However, information recently given to the writer verbally by J. Bjerknes, indicates that the radiative transfer of heat is relatively unimportant in heating the lower layers of the atmosphere.

[8] J. Wyman, and collaborators, "Vertical motion and exchange of heat and water between the air and the sea in the region of the trades," Woods Hole Oceanographic Institution, 1946 (unpublished).

8. Summary and conclusions

The results indicate that approximately correct seasonal and annual values of the total heat energy available for atmospheric processes over the North Atlantic and North Pacific can be obtained from previously derived seasonal and annual values of Q_c and precipitation amounts for these areas. For the computations of the 10-degree square values (upon which the charts are based), the following formula has been used:

$$Q_{pc} = Q_c + L_t P,$$

where L_t has been taken equal to 585 cal gm^{-1}.

In the present brief paper it is possible to present only the winter and summer charts for Q_{pc}; the remaining seasonal and annual charts, together with more detailed analyses of results, will appear in a later publication. The latter paper will also present the precipitation data that enter into the computations of Q_{pc}.

Some of the more important conclusions to be drawn from the computations are that:

a. The rate at which total heat (Q_{pc}) is supplied to the atmosphere over the oceans is greatest in the equatorial regions, along the western sides of the oceans and, in the North Pacific, along the extreme northeastern coast. The regions of lowest heat transfer, in both oceans, are centered along the eastern coasts of the oceans in subtropical latitudes.

b. At the higher latitudes the maximum Q_{pc} values occur during the winter season, with minima during summer. In the tropical and equatorial regions, on the other hand, the maxima occur during summer and the minima during spring.

c. A comparison of the *mean zonal* Q_{pc} values during winter for the western North Atlantic with those obtained by Wexler, which show the heat acquired by the atmospheric layer between sea level and 10,000 feet during February, indicates an excellent agreement between the two sets of values arrived at by different methods.

d. A comparison between Wexler's February chart and the winter Q_{pc} chart shows, however, that important regional differences do exist. It is reasoned that the two sets of values should agree only in the absence of *net* vertical motion within the 3-km layer. The sign of the difference between the two values should indicate whether there is net convergence or divergence and the magnitude of the difference should indicate the amount of convergence or divergence.

Acknowledgments.—The writer wishes to gratefully acknowledge the helpful advice given by Dr. H. U. Sverdrup throughout the entire period of the investigation. The writer is also indebted to Dr. G. F. McEwen of the Scripps Institution of Oceanography and to Drs. J. Bjerknes and M. Neiburger of the University of California at Los Angeles, for their interest and criticism.

TABLE OF SYMBOLS AND CONSTANTS

c_{pv} = specific heat of water vapor at constant pressure

c_w = specific heat of liquid water

F_p = percentage frequency of occurrence of precipitation of any type

L_i = latent heat of fusion $\approx$ 80 cal g^{-1}

L_{iv} = latent heat of sublimation $= L_t + L_i$

L_t = latent heat of vaporization (cal g^{-1}) at centigrade temperature, t. ($L_t = 594.9 - 0.51t$)

n = number of days

P = rate of precipitation in g cm^{-2} per unit time (equivalent to cm of liquid water per unit time)

P_a = total annual precipitation (g cm^{-2} yr^{-1})

P_s = total seasonal precipitation (g cm^{-2} season^{-1})

Q_a = total rate of energy exchange between sea and atmosphere $= Q_e + Q_c$

Q_c = rate of exchange of sensible heat between sea and atmosphere through convection

Q_e = rate at which heat is used for evaporation

Q_p = rate at which sensible heat is released to the atmosphere through the condensation and precipitation of water vapor

Q_{pc} = rate at which total heat is supplied to the atmosphere through the exchange of sensible heat with the sea surface and through the condensation and precipitation of water vapor $= Q_p + Q_c$

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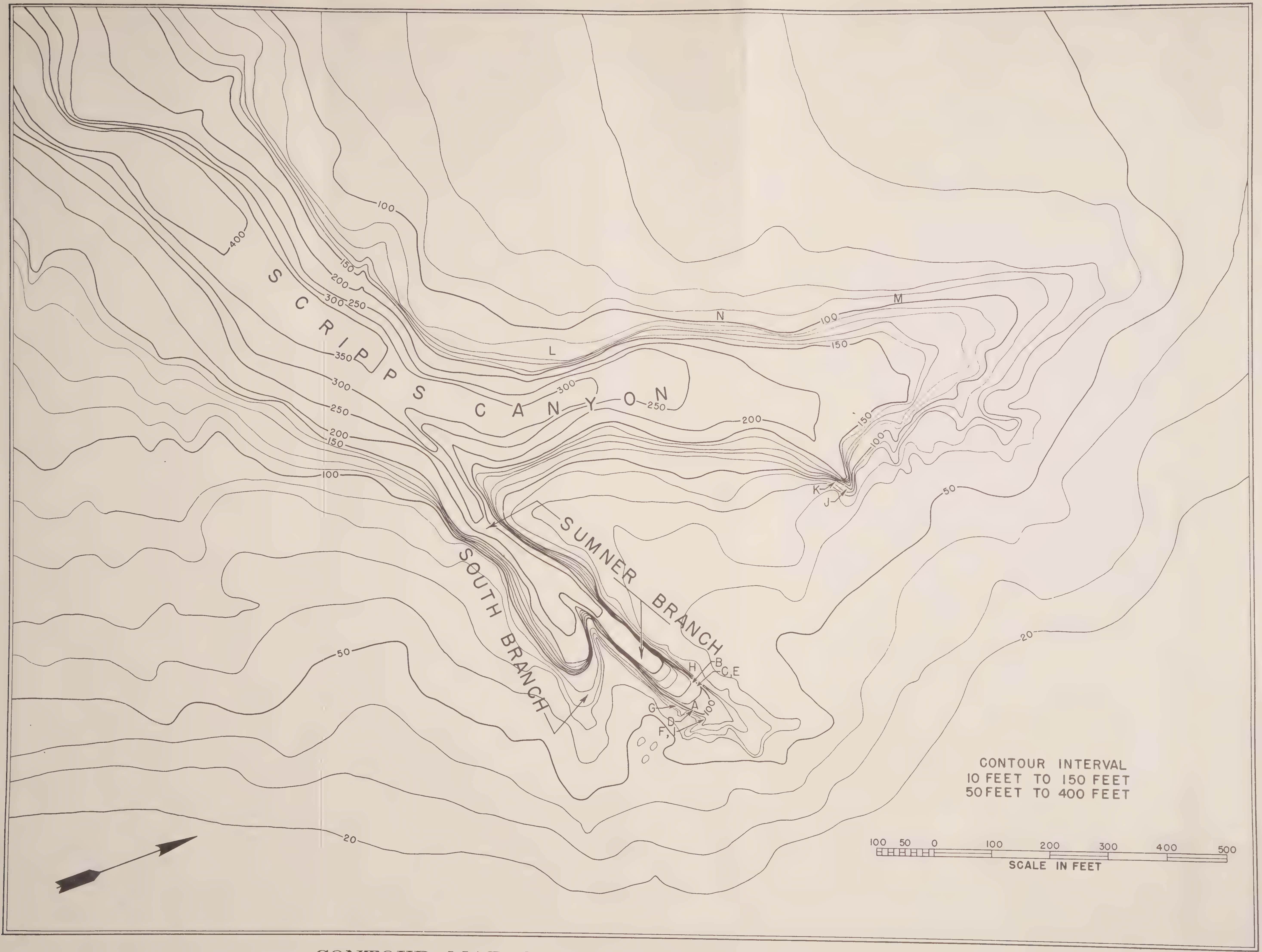
Contribution No. 429


SCRIPPS CANYON
SUMNER BRANCH
SOUTH BRANCH
400
350
300
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200
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J
A
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C, E
D
F
G
H
CONTOUR INTERVAL
10 FEET TO 150 FEET
50 FEET TO 400 FEET
100 50 0 100 200 300 400 500
SCALE IN FEET

CONTOUR MAP OF HEAD OF SCRIPPS CANYON

Although map is based on thousands of soundings it probably does not show many of the intricate features of the sea floor in this area. Note vertical cliffs and the flat but steeply sloping valley floors. Letters give location of photographs. Note also change in contour interval at 150 feet.

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TERRESTRIAL TOPOGRAPHY OF SUBMARINE CANYONS REVEALED BY DIVING[1]

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ABSTRACT

To obtain more detailed information concerning the nature of submarine canyons, diving operations were carried on in the heads of two typical canyons in the La Jolla area. Frank Haymaker, who dove under the writer's telephonic direction, described and photographed features which show that these canyons closely resemble the adjacent land canyons. Haymaker found vertical and even overhanging rock walls, narrow tributaries entering either at grade or as hanging valleys, and sediment-covered canyon floors. Cliffs of alluvium with layers of cobbles were discovered at the head of one of the canyons. In none of the 62 dives, extending over a period of a year, was there any evidence of significant density currents nor of the effect of any other strong currents moving down the canyon floors. The evidence suggests that the canyons were excavated by streams and that the heads are being filled but

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[1] This work represents in part the results of research carried out by the Office of Naval Research, the Hydrographic Office, and the Bureau of Ships under contract with the University of California.

that the fill is removed from time to time by mud flows. Although the dives did not go deeper than 190 feet in the canyons, evidence is presented to show that the topography could not be due to moderate lowering of sea level.

INTRODUCTION

In October 1946 Frank Haymaker, anaturalist and former Navy diver, made the first dive into the submarine canyons of the La Jolla area (Fig. 1), 12 miles north of San Diego. Landing on the east wall of Scripps Canyon just above a vertical cliff, he described through the two-way telephone system a scene of extraordinary beauty as well as of great interest to an investigator of submarine canyons. The remarkable clarity of the water, giving a visibility of about 30 feet on the bottom, gave great promise for photography in the canyon heads. However, this water clarity proved to be most exceptional; despite 55 intervening dives, no such water was seen again until January, 1948, when a 9-day period offered ideal conditions. Prior to this time dives yielded some photographs and indicated the points in the canyons where photographs would prove particularly worth while if the water cleared. Also this earlier period gave an opportunity to get the photogrraphic equipment working smoothly and to learn the most efficient methods. Shortly after the January period of clear water ended, the operation was forced to an end by a northwest blow which hit with little warning and caused the loss of the 38-foot boat used in the dives and the greater part of the diving equipment.

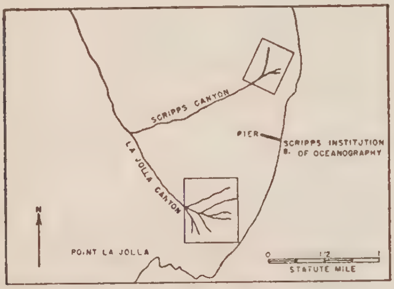


FIGURE 1.—AXES OF THE LA JOLLA CANYONS

Areas of Plate 1 (head of Scripps Canyon) and of Plate 8 (head of La Jolla Canyon) indicated.

The photographic portion of the diving operations was only one of several investigations. For example, the interpretation of the photographic results and of the telephonic descriptions given by the diver required a large amount of soundings to form a general picture of the areas in which the diver was operating. Also a study was made of rocks, marine sediments, and alluvium collected by the diver from canyons. Other activities such as current measurement and coring of the canyon floors were carried on only to an extent sufficient to warrant passing mention in the present report.

The investigation of the canyon heads by diving operations is not without economic application. In recent years, jetties for three California harbors have been built directly into the heads of submarine canyons. Relative to beach erosion and to the fate of the harbor jetties, it has become important to determine both the exact nature of the canyon heads and the processes operating in the canyons.

ACKNOWLEDGMENTS

The diving investigation of the La Jolla canyons was made possible by funds from the Penrose bequest of The Geological Society of America and from Navy contracts with Scripps Institution. The skill and zeal of Frank Haymaker in getting the photographs, many of them in most difficult diving terrains, and the detailed descriptions by Haymaker of the areas were of the greatest possible help. Haymaker had majored in zoology at the University of California at Los Angeles and during his association with Scripps Institution of Oceanography made a considerable study of geology in order to improve the accuracy of his description of geological features which he encountered on the bottom. The photographic enlargements of the 25-mm films used in the submarine photography were largely the work of Haymaker, and his skill in "dodging-in" the important features added greatly to their value. The dive tending by D. B. Sayner and R. L. Wisner soon became so professional that the operations moved with far greater smoothness than could normally be expected from amateur dive tending. Acknowledgment should also be made of the effectiveness of the Ewing submarine camera devices which were used for most of the work. These were equipped with handles and a rack for flashlight bulbs, the latter devised by Haymaker. Thanks are due Dr. Roger Revelle for many helpful sug-gestions in the manuscript.

Nature of Operations

Diving into a narrow submarine canyon which has vertical and even overhanging walls is a hazardous undertaking. It requires careful investigation of depths and surface currents prior to anchoring, and the laying of both bow and stern anchors in such places that they will not slide down into the canyon. The location for the dive is predetermined by a combination of ranges and sextant angles, a buoy with short scope is dropped and then the anchors are lowered and the boat is jockeyed into position by manipulation of the anchor lines at either end of the boat. Care had to be taken to avoid anchoring at points where rip currents were in evidence since the changing currents in the outer ends of the rips cause considerable shift in position of the boat, endangering the diver's lines.

The writer directed the dive operations through two-way telephones. When Haymaker reached the bottom he would report on the state of visibility. When the visibility was fair but too poor for photography, the diver would walk around the bottom looking for features which might permit future photographs. Such features were located as closely as possible by the amount of the life line which was out and the direction in which the diver's bubbles were rising. When interesting rocks were discovered, a skiff was rowed over to the diver and a sledge hammer and a chisel lowered so that he could break off the rocks and send them up in a bag. Breaking off rock under the surface is not easy since it is difficult to swing a hammer, but in general the diver was able to obtain fragments. Haymaker obtained samples of the fill on the canyon floor by driving in pipes. The personnel at the surface would pull out the pipe, and Haymaker would tie a cover over the pipe end to hold in the sample. It was difficult to obtain long cores because of the presence of hard packed sand. A more effective coring means is being built for future operations.

Directions during the dives were obtained from a compass worn on Haymaker's wrist. At frequent intervals Haymaker gave the direction and relative velocity of the bottom current and the nature of the bottom surge. When the current was too weak to be determined from the movement of floating debris, it was observed by allowing a line, with the end weighted so as to have zero buoyancy, to float out from the diver. The use of special instruments for further current work on the canyon floors is being planned.

In bottom photography an attempt was made to use a camera mounted on a tripod, but the setting up of the tripod frequently stirred up so much sediment that photography was very ineffective. Also the time required to set up the tripod greatly interfered with the making of a complete photographic record. By holding the Ewing camera case in his hands Haymaker could keep ahead of his own murk and could take 10 times as many photographs as were possible with a tripod. The location of each photograph was noted as closely as possible, and the diver's description was recorded.

Murkiness in Canyons

The diving operations into the canyon heads were greatly hindered by the murkiness of the water. Day after day the water had just enough silt or plankton so that the tributaries, the overhanging rocks, and the vertical cliffs described by the diver would fail to register on the films. An extreme contrast was noted on a day when the water on the shelf at the side of the canyon was so clear that we could see bottom in 55 feet of water. At the canyon rim the diver could see only about 10 feet. Looking down into the canyon Haymaker found that the murk was general.

The turbidity in the canyon heads is attributable in part to suspended sediments, derived from the washing away of the shale and mud at the base of the wave-cut coastal cliffs, and in part to plankton. The murk in Scripps Canyon was almost always bad after spring tides when the waves reached the base of the coastal cliffs shoreward from the canyon. It was, of course, also bad after all periods of large waves. The effect of the runoff after the very mild rain storms which occurred during the 15-month period of diving operations was not very great. So far as could be told, most of the mud moved out over the surface and soon disappeared without settling into the canyons. The mud washed from the cliffs and carried out by rips gravitated slowly toward the canyon, and the gentle back-and-forth currents appeared to be just sufficient to keep particles in suspension along the canyon bottom.

It had been supposed that in summer after the end of the stormy season the water in the canyons would clear, but unfortunately when the waves had gone down the plankton had so increased that the water was as murky as ever. At times the plankton were in layers, making it possible to operate in clear water below the cloudy layer.

Finally, in January 1948 the plankton had disappeared, and the waves were small so that the water at last cleared. The period of clear water in all of the canyon heads began at a time when the bottom currents had apparently ceased.

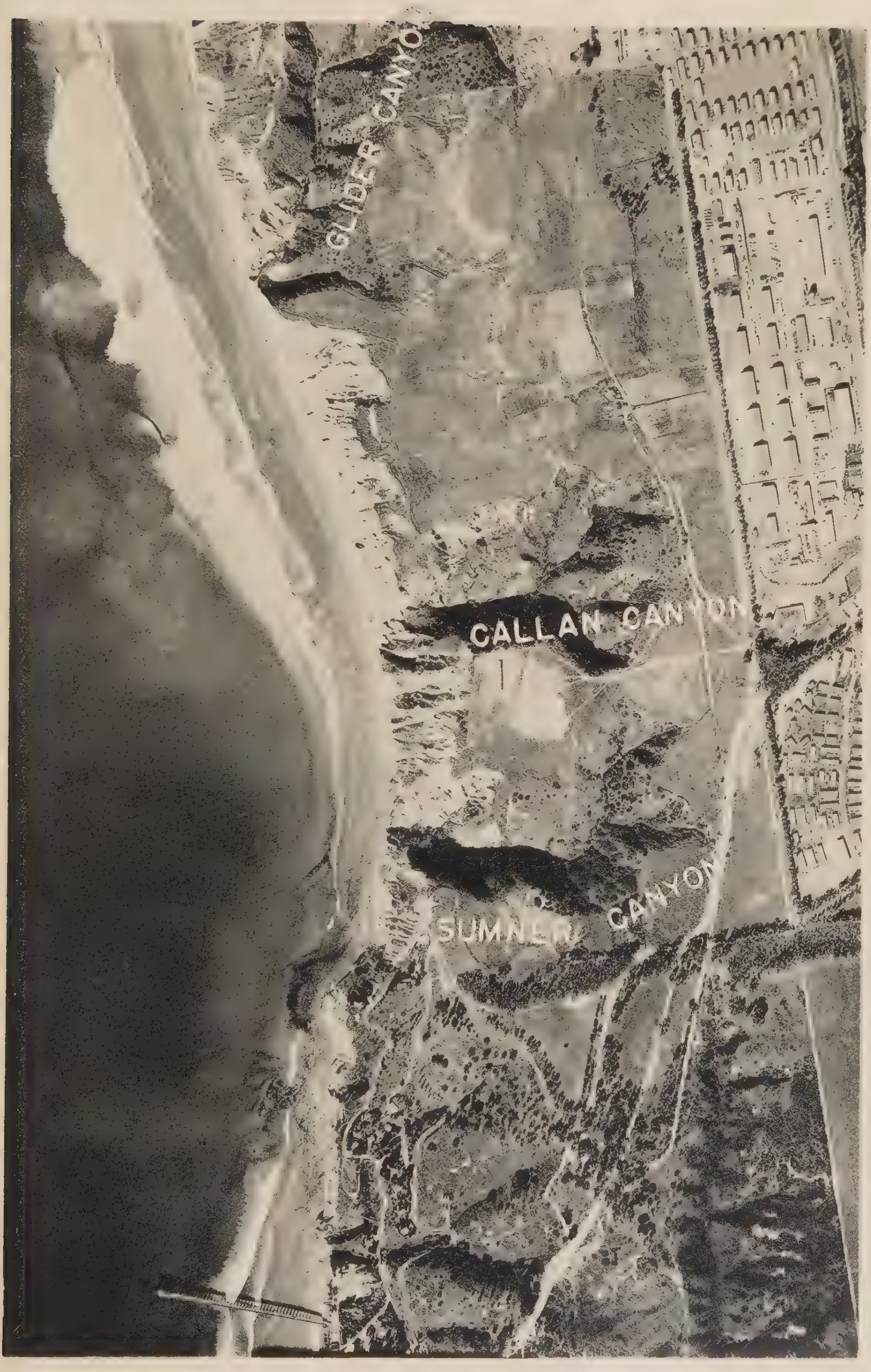
Scripps Canyon

General Topography

In 1934 Scripps Canyon was surveyed in considerable detail by wire soundings. At that time echo sounding was completely out of the question because (1) the sonic sounders available could be used only on large vessels which could not possibly maneuver into the near-shore positions at the head of the canyon, (2) the machines lacked recording devices which are essential to pick up details, and (3) the walls proved to be so steep and the base so narrow that the wide cone of the sound "beam" would bring in echoes from walls alone rather than from the floor of the canyon. Today, the first two difficulties have been removed, but the third still remains although soon Bottom Scanners (Russell, 1946) may give us correct profiles along the axis of the canyon by sound. Meantime, we have been using a recording echo-sounding device which attaches to the 38-foot buoy boat used in the diving operations. With this instrument, considerable mapping has been possible for the canyon heads and less precipitous portions of the walls. The instrument shows the presence of tributaries, many of them only gullies, which are difficult to pick up by the much more laborious process of wire sounding. Furthermore, echo soundings make it easily possible to prove the actual existence of any feature by running repeat lines along ranges on the same day. This is important since occasional false echoes may come either from schools of fish or from some temporary defects in the electronic system.

The accompanying map (Pl. 1) of the head of Scripps Canyon and of its two main tributaries is by no means perfect, but it is probably at least as good as most surveys of land canyons. Recent discoveries indicate that there are more tributaries and more vertical walls than had been supposed. Probably further soundings will show that there are even more of these features. Examination of the contours indicates that the canyon has three main tributaries at its head. The southern two branches extend shoreward to depths of about 16 feet and to within about 500 feet of the average low tide line on the beach. They are both located almost directly off Sumner Canyon (Pl. 2), a profound valley which cuts into the 300-foot sea cliffs in the vicinity. The inner portions of these tributaries are gently sloping, sand-covered valleys which have floors and walls with so little relief that it is not detectable by a diver. They both show a sudden change in gradient at axis depths of about 75 feet for South Branch and 50 feet in Sumner Branch. Beyond this the gorgelike character of the canyon begins, and rock appears on the walls. At depths of 100 feet, Haymaker determined that the floor itself was comparatively flat and covered with sediment despite its high gradient of about 25°. The two tributaries join at a depth of about 230 feet; they are separated higher up by a knife-edge ridge. Wire soundings were most difficult to obtain near the juncture of these two canyons because of the precipitous slopes and the large error resulting from the lead line being even a few degrees out of plumb.

The northern head of Scripps Canyon extends in to within 800 feet of the cliffed shore line, terminating near the mouth of Callan Canyon, the most impressive land canyon of the district (Pl. 2). The head of this main branch of Scripps Canyon has a depth of about 50 feet. Like the other branches it deepens precipitously, dropping at least 50 feet in 100 feet beyond the 57-foot depth. So far as is known, all of the outer canyon has an incised inner gorge with clifflike walls which extend to the bottom of the canyon. In addition to Sumner Branch, which comes in at grade, the southeast wall of the main canyon has a series of tribu-


GLIDER CANYON
CALLAN CANYON
SUMNER CANYON

AIRPLANE VIEW OF SEA CLIFFS AND LAND CANYONS INSIDE SCRIPPS CANYON

Rip currents which supply fine suspension sediments to the waters within the canyon base are shown to the right.

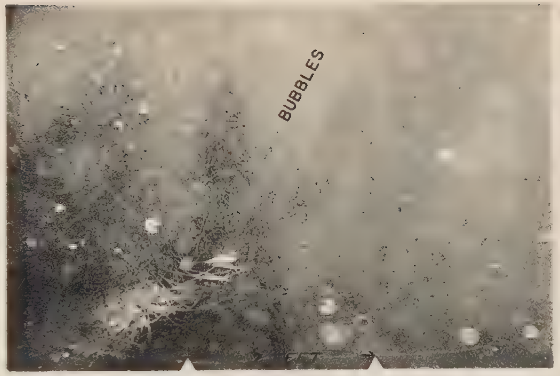


FIGURE 1. COLUMNS OF GAS BUBBLES RISING FROM FLOOR OF SUMNER BRANCH

The bubbles are the milky zones rather than the round objects which are due to reflected light from suspensions in the water. Depth 100 feet. Location at A, Pl. 1.

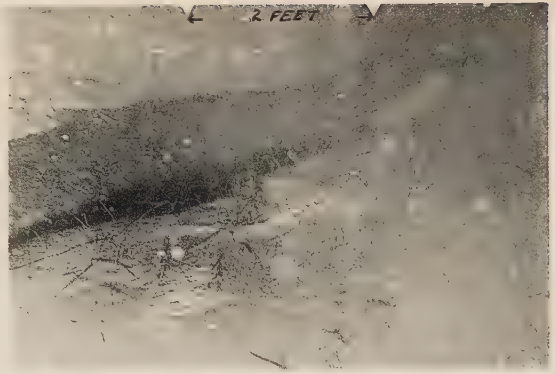


FIGURE 2. SHALLOW GULLY AT BASE OF CLIFF ON NORTH SIDE OF FILLING OF SUMNER BRANCH

Depth 100 feet. Location at B, Pl. 1.

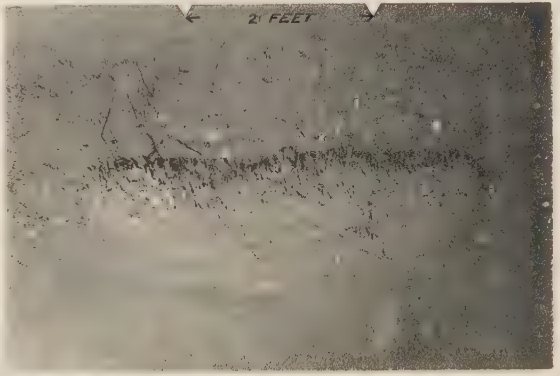


FIGURE 3. CONCRETIONARY LENS PROJECTING FROM VERTICAL WALL ON NORTH SIDE OF SUMNER BRANCH

Depth 100 feet. Location at E, Pl. 1.

FIGURE 4. LARGE OVERHANGING MASS OF ROCK ON SOUTH WALL OF SUMNER BRANCH

Photo taken from floor of tributary valley. Projecting mass is directly above portion of cliff shown in Pl. 5, fig. 1. Depth 80 feet. Location at F, Pl. 1.

SPECIAL FEATURES OF SUMNER BRANCH

tary valleys many of them hanging. The northwest wall, however, is largely free from tributaries in the inner portion.

Dives into Sumner Branch

Thirteen dives were made into Sumner Branch. The early ones indicated the existence of remarkable features, but great difficulty was found in obtaining good photographs. The dives on January 21 and 23, 1948, into the head of Sumner Branch were sources of great excitement to both diver and surface party since even the area at the canyon bottom, which always had been blanketed in murk, was remarkably clear, and the features which had been so hard to describe previously now became vividly apparent. Because of faulty film the pictures on January 21 did not come out, but those taken on January 23 are satisfactory. Haymaker followed the same route as previously. His description over the phones during these two dives gave a very clear idea of the area, agreeing with the photographs in almost every respect. The diver landed on the canyon floor which he described as sloping seaward at about 20° and being comparatively smooth. The floor was thickly covered with eel grass and kelp. Bubbles[2] were seen rising in large quantities (Pl. 3, fig. 1). We could, of course, see them at the surface. The floor proved to be about 40 feet across. On the north side, Haymaker observed a gully which looked like a gutter on the side of a road. It was about 2 or 3 feet across and 8–10 inches deep (Pl. 3, fig. 2). The gully floor lacked all signs of current ripples. It could be traced for at least 30 feet along the base of the cliffs on the north side. Nothing like it was seen on the other side or in the center. The canyon floor on these occasions was fairly firm so that Haymaker sank into it only a few inches. He had described the same floor as very soft during a previous dive on August 28, 1947. The explanation can be assumed to be either compaction during the interim or the sliding out of the top of the fill.

The contact between the fill on the floor and the canyon walls in this area is shown in Plate 4. The rock walls rise vertically from the floor. Haymaker described the rock stratification as horizontal in this particular section, which allows one to judge the angle of contact with the fill. The nine available photographs show that this angle ranges from a slight back slope to 45° down canyon with the majority sloping about 15° to 20° down canyon. Since the floor was described as fairly uniform in its down-canyon slope, either the floor material in slumping down canyon has left irregular contacts along the side or material falling from above has built small fans at the base. The existence of such fans was not supported by most of Haymaker's observations although he thought he saw one example below a hanging valley.

Probably the canyon fill comes largely from the canyon head. If the fill came from sliding of sediment over the vertical walls, fans should be abundant at the base of the cliffs.

The walls are well stratified (Pl. 4). Concretionary lenses project as overhanging masses (Pl. 3, fig. 3). Most of the large overhanging masses consist of resistant formations (Pl. 3, fig. 4). Prominent joints are indicated in some of the photographs. Pholad borings are shown in most of the pictures (Pl. 4) and were found in the rocks which were recovered. Unfortunately not many rock samples are available from this area, because emphasis was put on obtaining photographs during the January dives, and it was difficult to break off some of the projecting rocks on a previous occasion. The rocks from the top of the cliff are impure limestone with a high percentage of silt and sand grains in the insoluble residue. This rock is a member of the Eocene Rose Canyon shale formation (Hanna, 1926).

In the vicinity of the photographs, the cliffs are about 40 feet high. The vertical portion of the cliffs increases in height outwardly until it is over 100 feet near the juncture of Sumner and South branches. The slope above the cliffs is variable but in general not very steep. On the edge, there are projecting masses of rock partly covered with Gorgonia corals and other growths. Elsewhere small nicks or gullies cut the rock (Pl. 5, fig. 1). Above the rocky edge is a sand slope, which was always observed to be deeply ripple marked. At one place well out on the north rim the ripples terminate at the very wall of the canyon (Pl. 5, fig. 2).

At the head of the rock gorge three gullies come down into the canyon at steep gradients on either side and enter at grade. A photograph was taken from the 30-degree sloping floor of one of these tributaries looking toward the main canyon (Pl. 5, fig. 3). The vertical character of the canyon wall is clearly indicated. Rock from the tributary wall proved to be shale despite the vertical slopes. Haymaker followed up this tributary to where it ended on the divide between Sumner and South branches. From there he walked west until he came to another narrower tributary which was about 20 feet across at the top. He followed this to a point where it terminated as a hanging valley on the edge of the clifff. Like the main valley, these tributaries were floored with eel grass and kelp mixed with fine sediment, mostly sand. Other tributaries cut the top of the cliff on the north side. No opportunity was found to trace these tributaries downward, so it is not known whether they enter the main canyon at grade or as hanging valleys. One of them had a gradient estimated at 45°.

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[2] The bubbles probably consist of methane gas. They were first observed in 1937.

On the ridge between Sumner and South branches, Haymaker described a sand floor with an undulating surface suggestive of sand dunes or giant ripples with height of 6–10 feet. Unfortunately, no photograph shows these features although several kodachromes showed small sand ripples in the foregound with only a hazy indefinite background.

Dives onto Walls of Scripps Canyon

Haymaker made 12 dives onto the walls of Scripps Canyon, all of them located near the break in slope which descends to the canyon floor. In the areas visited, the floor was of the order of 200 feet deep, and on most occasions the murk appeared considerably worse below the break in slope than above, so that it was not thought advisable to take the large risk of such a deep dive. Above the break the visibility was ordinarily better than at corresponding positions in Sumner Branch nearer the shore.

On the southeast side of the canyon, the sandy slope leading to the steep inner gorge is broken in places by rock outcrops. Near the edge the rock is quite continuous and is covered with a luxuriant growth of organisms. On the upper slopes where the depths varied from 75 to 120 feet, ripple marks were reported only in the bottom of a gully. These ripples crossed the axis of the gully and indicated a moderately strong current moving either up or down the axis.

The break in slope of the southeast side of Scripps Canyon is irregular. Gullies cut the upper slope at each locality visited on this side of the canyon. The only successful photograph of a gully (Pl. 5, fig. 4) shows a narrow ravine with irregular rock slopes largely covered with a growth of Gorgonia corals and other organisms. The gullies steepen at the edge to as much at 60°, and at least one of them terminates as a hanging valley. Along the edge of the cliff between the gullies, a considerable number of jutting rocks were observed. Haymaker photographed them by leaning out over the precipice and being supported by his life line.

Because of the extremely clear water at the time of the first dive in 1946, Haymaker was able to look down the cliffs for about 40 feet. He could see the layers of rock dipping down canyon to the southwest at an angle of about 10°. Measuring the cliffs with an inclinometer showed that they averaged about 80° but had distinct overhangs in many places. Farther out along the axis of the canyon the heights of these cliffs range up to about 250 feet. In the area where the dives were made the heights average about 100 feet. Unfortunately nothing is yet known of the contact between the base of the cliffs and the canyon floor. The only rock samples obtained from the southeast wall were sandstone considerably bored into by pholads, but soft shale was found above the break in slope.

The northwest wall of Scripps Canyon was the site of seven dives. These covered a length of 900 feet above the break in slope, and one extended across the shallow head of the canyon. Visibility was never very good during these dives so that only a few satisfactory photographs are available. The slope steepens toward the cliffs and becomes progressively more rocky. To the southwest, the slope above the cliff is covered with huge rocks which made it difficult for the diver to proceed. The growth of Gorgonia is most abundant in this area and is almost forestlike in appearance (Pl. 6, fig. 1). Growth extends out to the brink of the canyon. Farther up canyon to the northeast, the slopes are less rugged and have sand-covered terraces

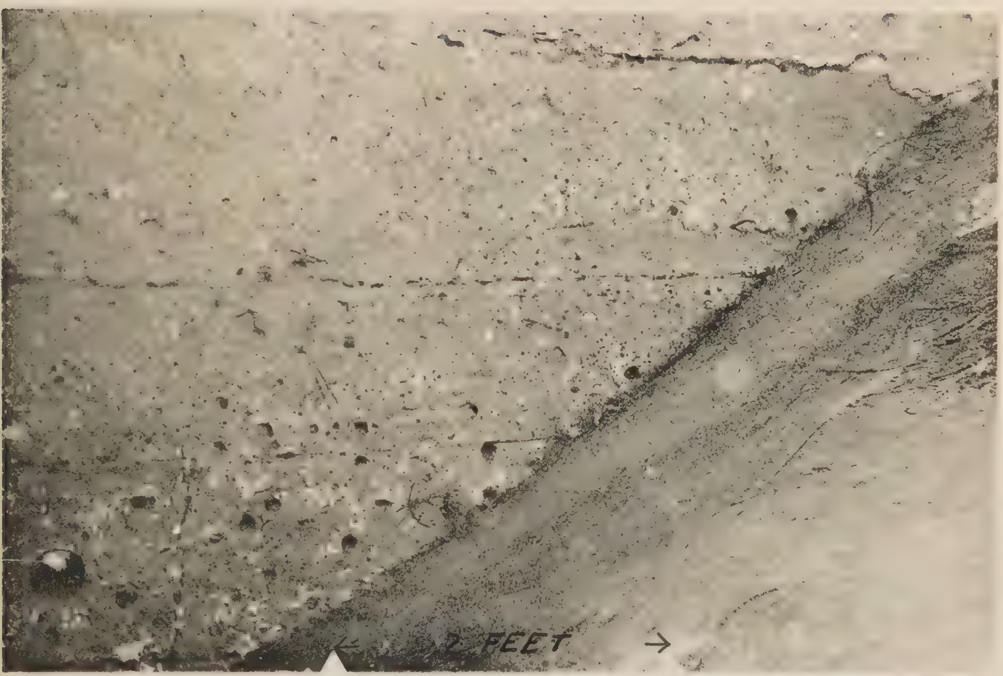

FIGURE 1. CONTACT OF NORTH WALL OF SUMNER BRANCH WITH FILL ON CANYON FLOOR
Rock face is vertical. Note pholad borings. Depth 95 feet. Location at C, Pl. 1.

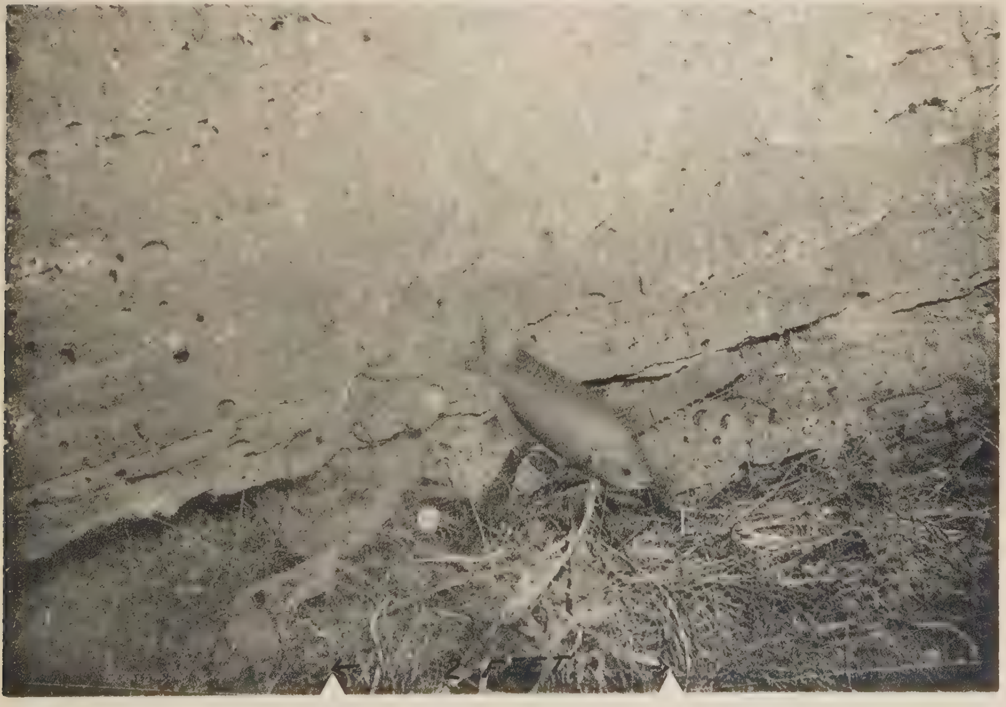

FIGURE 2. CONTACT OF SOUTH WALL OF SUMNER BRANCH WITH FILL ON FLOOR
Note that angle is quite different from that of Figure 1. Great abundance of kelp and eel grass also illustrated. The fish is a Blacksmith (Chromis punctipinnis). Depth 100 feet. Location at D, Pl. 1.

FLOOR AND VERTICAL WALLS OF SUMNER BRANCH

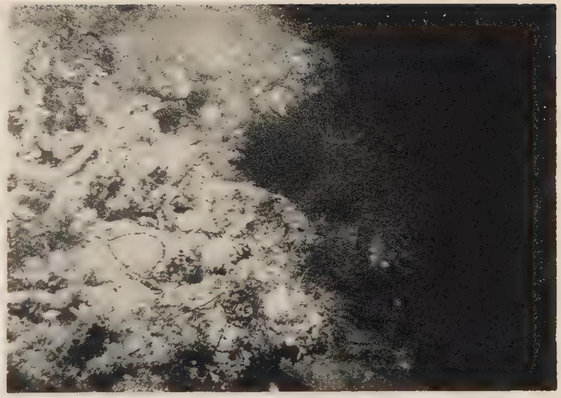

Figure 1. Small Gully in Upper Edge of Cliff on South Side of Sumner Canyon
Depth 60 feet. Location at G, Pl. 1.

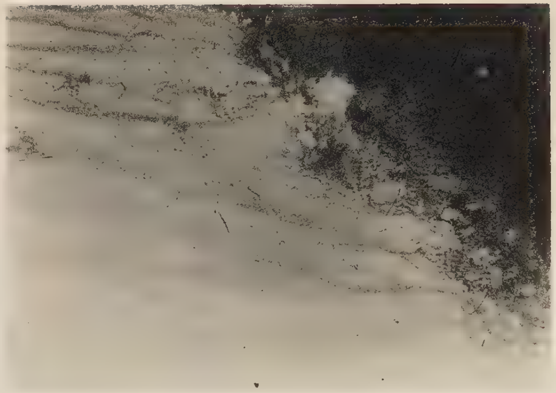

Figure 2. Ripple Marks in Sand Extending to Edge of Steep Slope of North Side of Sumner Branch
Depth 70 feet. Location at H, Pl. 1.

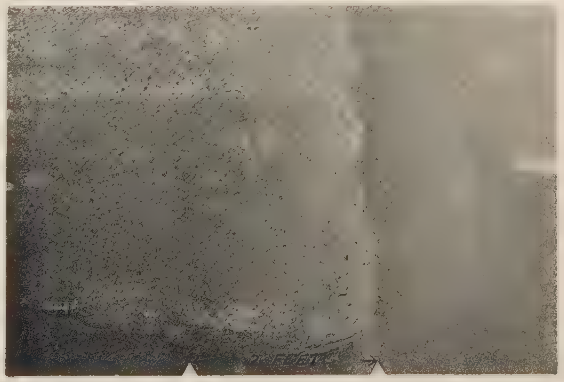

Figure 3. Vertical Cliff
Picture taken from steeply sloping floor of tributary near its juncture with main valley of Sumner Branch. The fish is a Blacksmith (Chromis punctipinnis). Depth 75 feet. Location at I, Pl. 1.

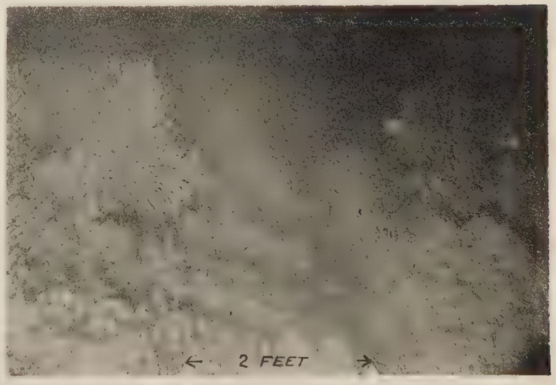

Figure 4. Gully Leading into Main Head of Scripps Canyon on East Wall
Note extensive Gorgonia growing on the rocks. Depth 90 feet. Location at J, Pl. 1.

TRIBUTARIES OF SUMNER BRANCH AND
SCRIPPS CANYON

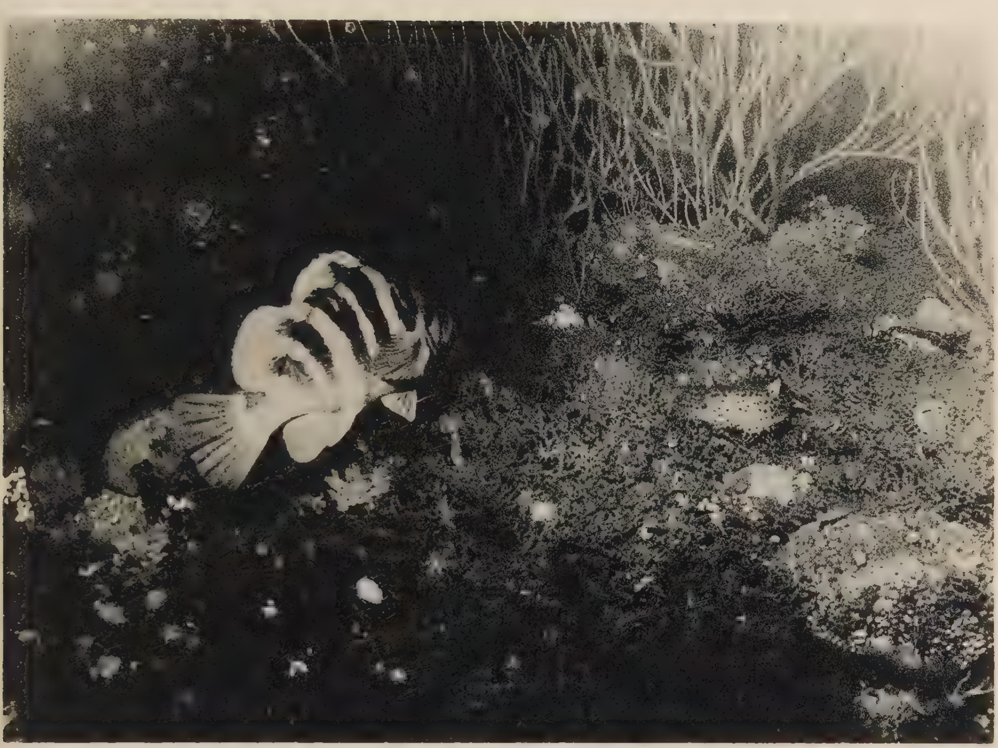

Figure 1. Rock Terrace on West Wall of Scripps Canyon
Note large size of the Gorgonia in the background. The fish (Sebastodes serriceps) and the holothurian (Stichopus californicus) were close to the camera. Depth 115 feet. Location at L, Pl. 1.

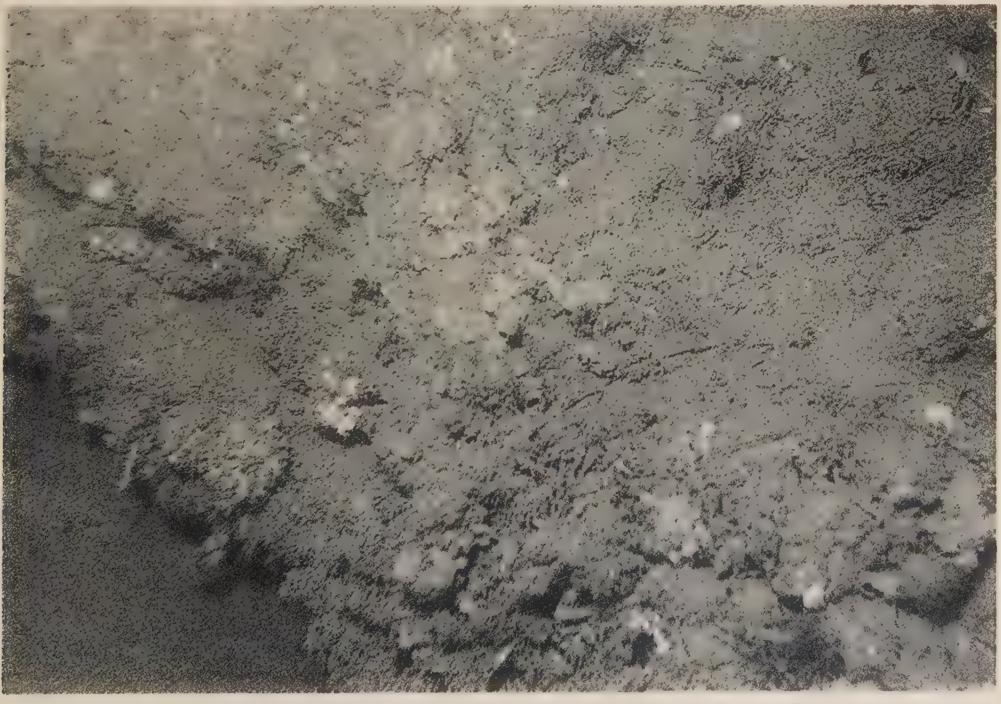

Figure 2. Rock Slope and Sand Terrace on West Wall of Scripps Canyon
Terraces provided easy progress along the steep canyon wall. Depth 90 feet. Location at M, Pl. 1.

TERRACES ON SIDE OF SCRIPPS CANYON

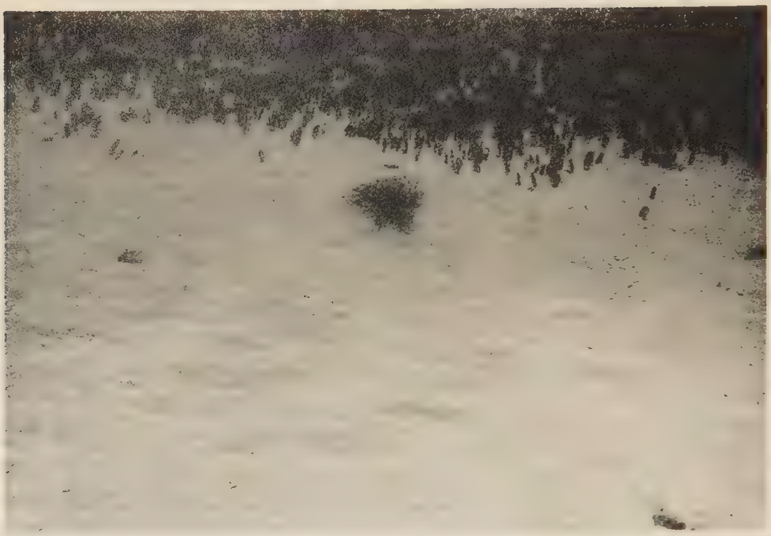

FIGURE 1. RIPPLE-MARKED SAND AT HEAD OF LA JOLLA CANYON
Note sand dollars (Dendraster excentricus) which are turned on edge and live in great abundance in this locality and at the head of Scripps Canyon. Depth 38 feet. Location at A, Pl. 8.

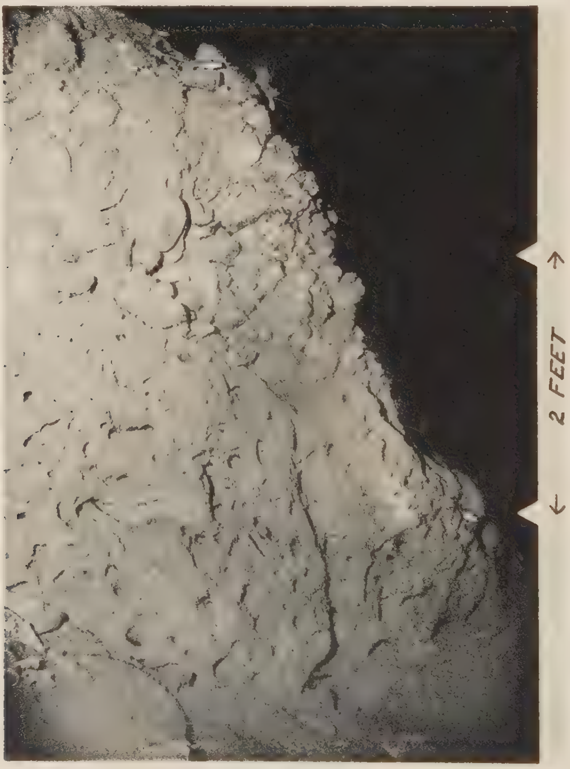

FIGURE 2. ALLUVIAL MATERIALS EXPOSED ON RIDGE BETWEEN TWO GULLIES AT HEAD OF LA JOLLA CANYON
Note abundant holes in sandy alluvium below cobbles. Gobies (Coryphopterus nicholsii) can be seen in the holes, and a sea anemone on the shoulder at the top of the picture. Depth 95 feet. Location at B, Pl. 8.

RIPPLED SAND AND ALLUVIAL FORMATIONS AT HEAD OF LA JOLLA CANYON

(Pl. 6, fig. 2), along which it was easy for Haymaker to progress. Walking northeast during a dive near the canyon head, Haymaker came onto a sand slope and crossed the canyon head above the rock gorge. Here the slopes are gentle. No ripples were reported from this sand area where the depth was 80 feet.

The break in the slope below the terraces is as spectacular on the northwest side of Scripps Canyon as in the other localities described above. Despite considerable walking along the edge, no good example of a gully was observed. Projecting rocks and slight rock benches were found. Also at a number of places the cliffs appear to be distinctly overhanding.

LA JOLLA CANYON

General Topography

Although the head of La Jolla Canyon is practically devoid of rocks, the topography is strikingly irregular (Pl. 8). At its head the canyon breaks off precipitately. In many places there is a descent of 100 feet in an equal horizontal distance. Vertical cliffs of small magnitude are common. There are large tributaries on either side, particularly to the north where two arms extend for over 1000 feet diagonal to the shore. One southern tributary is known as "Sea Lion Gulch" because during 6 months of the year a large colony of sea lions has chosen the head of this gully as their rendezvous. Ridges between tributaries are either knife-edged or rounded. The tributaries widen as they approach the main valley. The floor below the point where the tributaries join to form the main valley is comparatively flat although steeply sloping. The valley floor is about 200 feet wide at depths of around 180 feet below sea level but narrow at greater depth.

Dives in the Gullies at the Canyon Head

Twelve dives were made into the central portion of the canyon head, mostly among the gullies which abound in this area. Gentle-walled valleys are found in the shallow water with rippled sand slopes supporting an abundance of echinoids (Pl. 7, fig. 1). These gentle valleys terminate abruptly in steep-walled gullies. Haymaker described the descent of one of these gullies as being like sliding down an open drain. Vertical walls are common on the sides of these gullies (Pl. 7, fig. 2). Ridges between the gullies are narrow and irregular (Pl. 9, fig. 1). At the base of some of the cliffs there are distinct talus cones (Pl. 9, fig. 2).

The cliffs and steep walls of the gullies consist of alluvium, similar to the alluvium of the Pleistocene (or Recent) sea cliffs south of Scripps Institution. For the most part this material is a moderately compact, poorly sorted loam with a striking absence of marine organisms. It has numerous holes in which small fish (known as gobies) are living (Pl. 7, fig. 2). Some of the cliffs toward the center of the canyon head have beds of cobbles (Pl. 7, fig. 2; Pl. 9, fig. 2), which are predominantly of crystalline rock as are the alluvial cobbles on land in this area. Lack of stratification and jumbled appearance indicate that in both cases the cobble beds are the result of flood deposits. The marine cobble beds have a few boulders up to about 1 foot in diameter.

The bottom of the gullies is covered with muddy sand containing considerable kelp and eel grass. The proportion of plant debris increases outwardly to depths of about 130 feet beyond which it decreases. Some of these algae are also found on the shelves above the cliffs, and in places stalks of kelp hang over the cliffs looking like strands of rope.

At an axis depth of 185 feet, the canyon floor was different in appearance. Eel grass and kelp were not at all common (one ball of eel grass was found), and the floor was sand with only a trace of the silt which was so abundant in shoaler water. So far as could be seen in the restricted field of a photograph which was limited by the usual murk, the surface of the sand was bumpy, although the roughness was not sufficient to impede progress over the bottom. The consistency of the bottom material was described by Haymaker as being "lumpy but firm".

Sea Lion Gulch and the Hanging Valley

Herds of sea lions apparently like to have a meeting ground on the ocean at some point which they can identify even in the fog. Dr. Carl L. Hubbs and J. L. McHugh of Scripps Institution have observed that the sea lions of the herd which gathers in winter off La Jolla show a decided tendency to congregate in the same geographic locality 1000 feet out from the shore. We made detailed soundings at this locality and found that it was at the approximate head of one of the southern tributaries of La Jolla Canyon at a depth of only about 30 feet. On one day the water was so clear that using a waterglass we were able to observe the sea lions swimming around the canyon head. That their location is approximately the same during a fog was determined by listening to the barking of the sea lions during the fog from shore points directly inside the gathering ground. Therefore, they must use the submarine topography to reach their rendezvous.

Dives into Sea Lion Gulch showed that it has comparatively gentle walls but is definitely a gully with a narrow axis which could be followed by the diver. The axis of the valley has an abundance of shells and sand together with cobbles up to about 10 inches in diameter. Pens from squid are very common, being undoubtedly the remains of the food of the sea lions. Some of the cobbles may have been sea-lion gastroliths. The fact that the pebbles and cobbles include a surprising abundance of soft calcareous shale fragments, 30 per cent by count, the remainder being of crystalline rock, indicates that the material has not been subject to great transportation. Rocks taken by Emery (1941) from the stomach of a dead sea lion contained four rounded shale fragments out of a total of 23 pebbles. On the other hand, pebbles on the local beaches have almost no shale. The collections from Sea Lion Gulch contain rocks weighing up to 5 pounds, probably too large for gastroliths.

Following down Sea Lion Gulch to a depth of about 65 feet, Haymaker came to a cliff with a vertical drop of 5 feet (Pl. 10). The floor widened here so much as to give the impression that the gully did not extend farther down; later this was found not to be the case. The cliff which cuts the Gulch extends beyond the confines of the inner gully and can be traced in either direction for a total length of about 50 feet. It could be seen to die out into the even slope of the canyon side. Apparently there are two recesses into the cliff marking the position of two separate gullies which are cut off by the cliff. Cobbles were seen in Sea Lion Gulch both at the top of the cliff and on the floor below (Pl. 10 fig. 2). The cliff contains the same poorly sorted alluvium as that of the main head of La Jolla Canyon. Holes in the alluvium house abundant fish larvae, and an octopus was seen in one hole.

Phantom Dike Gulch

A small steep-floored tributary enters Sea Lion Gulch from the south near the point where the latter enters the main canyon. This tributary descends 100 feet in approximately 220 feet giving it an average gradient of 24°. In an early dive into this gulch Haymaker encountered the only rock outcrop of all the diving operations in the head of La Jolla Canyon.[3] He described the rock as forming a vertical wall about 1 foot high which extended up the northeast side of the gulch with all the appearance of a dike. He broke off a large piece of the rock, which surprisingly, proved to be a well-cemented, highly calcareous, poorly sorted sandstone with clear lines of stratification parallel to the flat sides, which according to Haymaker, formed the sides of the vertical wall. The camera was out of order during this dive, but the locality was carefully marked and was given high priority for future work. Returning during the remarkably clear water of January, 1948, Haymaker made two descents along the axis of the gully looking at the sides with the greatest of care, but despite the good visibility he was unable to find a trace of the rock. Careful study of the fixes and ranges leaves no doubt that Haymaker was in the same gully, but a search for the rock was made in the neighboring gullies, to no avail. The bringing up of the rock broken from the wall leaves no doubt of its having been there; the rock had disappeared, apparently having been covered by slides of the sediment from above despite its projection of almost a foot above the surroundings. The occurrence of a vertical formation in this area of horizontal or slightly inclined rocks is puzzling. An origin as a sandstone dike is somewhat unlikely because of the stratification. Possibly a layer from the walls had toppled over and sunk into the sediment in this position.

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[3] Rock has been dredged farther out in the canyon (Emery and Shepard, 1945).

Phantom Dike Gulch, named for the elusive rock wall, was found to be floored by sand and mud with an abundance of kelp and eel grass in the upper portions but the gulch floor has sand and mud alone lower down. Going down the axis, the walls steepen and are vertical in places (Pl. 11, fig. 1). At the lower end of the valley, in about 140 feet of water, the slope flattens, and the gully enters the main valley at grade. At this place a large block of alluvium about 4 feet across and 3 feet high (Pl. 11, fig. 2) was found resting where it had apparently stopped in a slide down the steep valley floor.

An examination of the relatively flat-topped ridges between gullies in this area showed an interesting assortment of organisms (Pl. 12, fig. 1). Along with echinoids and holothurians there was a large amount of kelp. Cobbles and angular rocks lie scattered over the surface.

South Wall of La Jolla Canyon

To the west of Phantom Dike Gulch, the tributaries become less common. Two dives were made onto the shelf at the edge of the canyon. The terrace above the break is covered with coarse sand having an abundance of broad-leaf eel grass (Zostera). There is an abrupt change in slope at the brink, and a comparatively smooth mud and sand slope extends down at an angle of approximately 45°. The sediment proved to be largely very fine sand with abundant mica and a moderate amount of silt. The abundance and variety of marine life were in contrast to the paucity in canyon floor samples. In a few places there were small pockets which appeared to be the result of slumping. In walking along this slope Haymaker started small slides in the muddy sand. Much of the disturbed material went into suspension. The muddy water thus formed started down the very steep slopes but was soon carried clear of the bottom, rather than continuing as a bottom-flowing current which some geologists would have expected. The general smoothness of the wall on these steep slopes is certainly surprising. However, no great thickness of sediment may exist here because the Emery-Dietz coring device penetrated only a few feet of sediment near the base of the slope before encountering a mass hard enough to smash the nose. It seems likely that these steep sediment slopes are only temporarily in repose and are subject to occasional slides.

BOTTOM CURRENT OBSERVATIONS

Very few quantitative data relative to bottom currents were obtained from the dives because of the necessity of concentrating on the photography and general description of the canyons. Haymaker did, however, note the amount of surge and the net transport of floating objects. When possible he estimated the velocity. The currents observed were found to reverse in direction at least once during the course of each dive (during a period of half an hour to an hour). That is, if the current was flowing down canyon at the beginning of the dive, it was later observed flowing up canyon. Of the total number of current observations, 47 per cent showed currents moving down canyon, 30 per cent up canyon, 7 per cent across the canyon, and 16 per cent cent showed no current. The slight excess of down-canyon currents may be due to suspension (density) currents set up by the diver's progress over the bottom. The currents measured in submarine canyons by instruments have included approximately as many up-canyon movements as down (Shepard, 1948a, p. 62, 63). On one occasion Haymaker estimated that the current velocity was almost half a nautical mile an hour, but the rest of the time the velocity was much lower. There was no evidence that the currents were stirring up the bottom, and the water was remarkably clear on the day when the current was estimated as being as high as half a knot (Pl. 11). If this velocity existed, it must have been much slower at the very bottom. The feebleness of the currents probably accounts for the general absence of ripple marks on the canyon floors. Except in very shallow water ripples were only found in one place, a hanging tributary to Scripps Canyon. The feeble currents also explain the silt in the sediment samples on the canyon floors in contrast to the clean sand which was usual on the terraces of the canyon walls. In the latter localities the shoaler depth allows more wave stirring and winnowing of the fine sediments. However, relatively clean sand was discovered at the deepest dive in 185 feet of water, in a locality which was below the areas of muddy and kelp-covered bottom.

A sediment trap (Pl. 12, fig. 2), which has fine mesh socks placed so that their open ends face in four directions, was placed by Haymaker in the head of La Jolla Canyon. Two days later it was brought in, and the sediment content of the socks was weighed. It was found that the bags which received sediment carried by up-canyon currents had 64 grams, while those exposed to down-canyon currents had 38 grams.

During the first part of the period of excellent water clarity, in January 1948, the currents were almost missing. However, during the latter part of this period the currents were observed moving down canyon with unusually high velocities and without the usual reversals. During this same period Dr. Walter Munk of Scripps Institution reported that the long-period waves (averaging about 15 minutes) which had been appearing regularly on the long-period wave (tsunami) recorder at Scripps Pier had disappeared. It will be of interest to look for further correlations between the canyon conditions and these long-period waves.

COMPARISON OF SUBMARINE AND LAND TOPOGRAPHY

It might be supposed that soundings of the submarine canyons would yield much better data than diving operations for comparing the canyons of the sea floor with those on land. While it is true that soundings are the only method of bringing out the major canyon features, it is almost impossible to pick up small but important details by them. For example, we knew that there were very steep slopes in Scripps Canyon from the wire soundings, but it took an on-the-spot observer to find that these slopes included actual vertical and even overhanging cliffs, hanging valleys, and steep tributaries entering at grade. The diving operations were confined to the upper portion of the La Jolla canyons, but there seems to be no evidence from the soundings that the canyon characteristics change appreciably until much greater depths are reached. Therefore, it seems reasonable to assume that the dives have yielded us evidence of the detailed character of a considerable portion of typical submarine canyons.

The sea cliffs north of Scripps Institution have a series of canyons which are cut below the surrounding terrace to depths comparable to those of the submarine canyons where diving operations took place. Also the land canyons are cut into the same types of Eocene rocks as the branches of Scripps Canyon. Furthermore, the heads of the land canyons are cut into alluvium which resembles that of the head of La Jolla Canyon and its tributaries. The comparisons between the two types of canyons are accordingly of considerable significance.

The general resemblance of the drainage pattern of Scripps and La Jolla submarine canyons to the adjacent land canyons has been discussed elsewhere (Shepard and Emery, 1941, p. 59). The canyon trends show the same right-angled bends and even the same two principal axial directions. The comparison extends even to the details.

A general view of the land canyons is provided by an airplane photograph (Pl. 2), which may be compared with the generalized map (Fig. 1), the contour maps (Pls. 1, 8), and with the block diagram of Sumner Branch which Donald Sayner has prepared from data from the diving operations and the soundings (Fig. 2). The general resemblance between the land and the sea-floor topography seems to be unmistakable. The many branched heads found in both of the submarine canyons are also found in all of the land canyons. Both the land and the submarine canyons have many more tributaries in the upper reaches than lower down. Stretches of straight walls found in the land canyons (Pl. 2) compare with the ungullied northwest slope of Scripps Canyon.

Vertical cliffs like those of the submarine canyons are not uncommon in the land canyons (Pls. 13, 14). Tributaries enter either at grade or as hanging valleys in the land canyons and sea canyons alike (Pl. 13). Steps are found along the course of the land gullies (Pl. 13, fig. 2) just like the steps in Sea Lion Gulch. Jutting rock masses project from the cliff faces in the land canyons (Pl. 14, fig. 1) as do the jutting rocks of the submarine canyons. Projecting spurs are found in the alluvium along the course of the land valleys (Pl. 13, fig. 3) very much like the spur at the head of La Jolla Canyon (Pl. 9, fig. 1).

There are, on the other hand, some con-

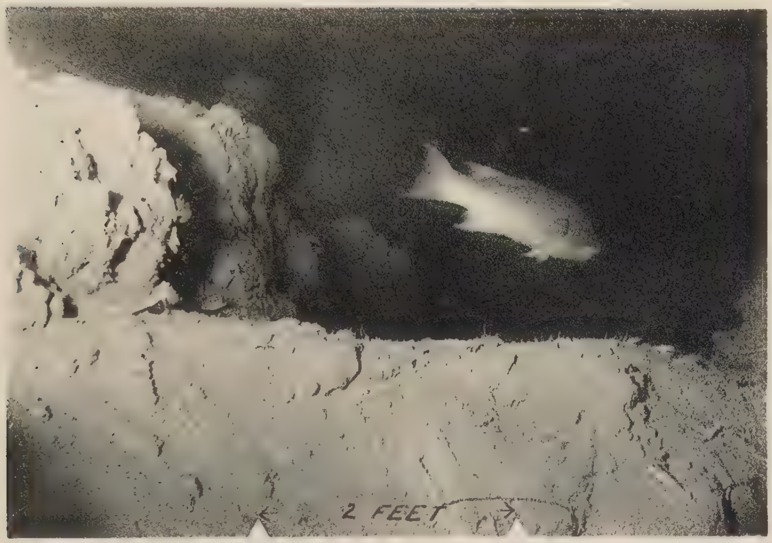

Figure 1. Flattened Portion of Ridge

Above Pl. 7, fig. 2. Compare Pl. 13, fig. 3. Larger fish, a California sheepshead (Pimelometapon pulchrum), and the smaller fish, a goby (Coryphopterus nicholsii) were abundant in this location. Depth 75 feet. Location at C, Pl. 8.

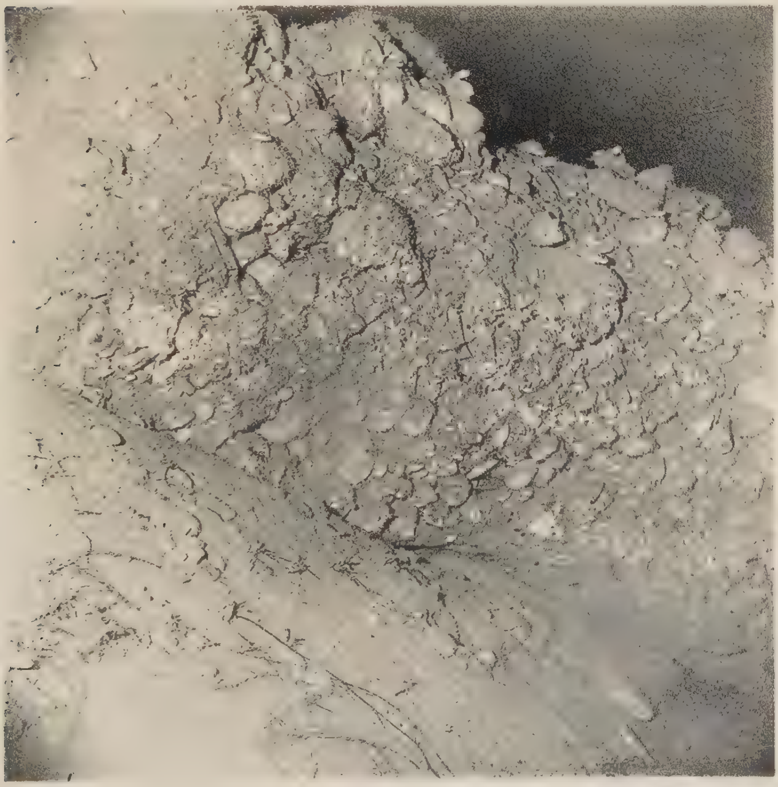

Figure 2. Contact of Cobble Bed at Head of La Jolla Canyon with Talus Slope

Note jumbled mass of cobbles indicative of flood deposition. Depth 90 feet. Location at D, Pl. 8.

RIDGES AND COBBLES AT HEAD OF LA JOLLA CANYON

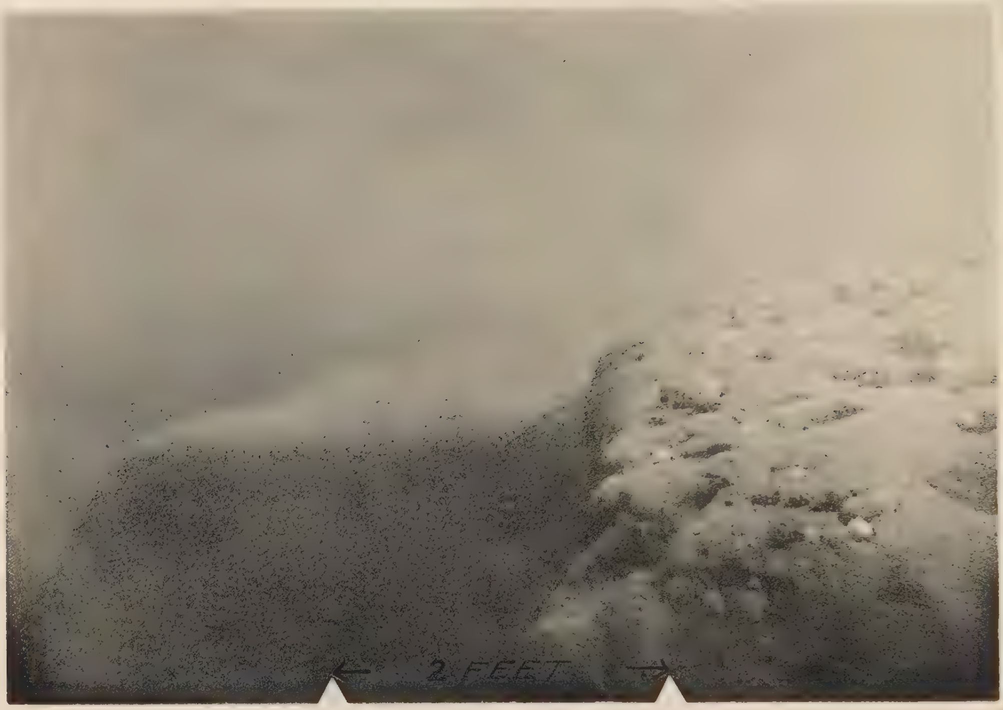

FIGURE 1. HANGING VALLEY IN SEA LION GULCH
Compare with Pl. 13, Fig. 2. Depth 65 feet. Location at G, Pl. 8.

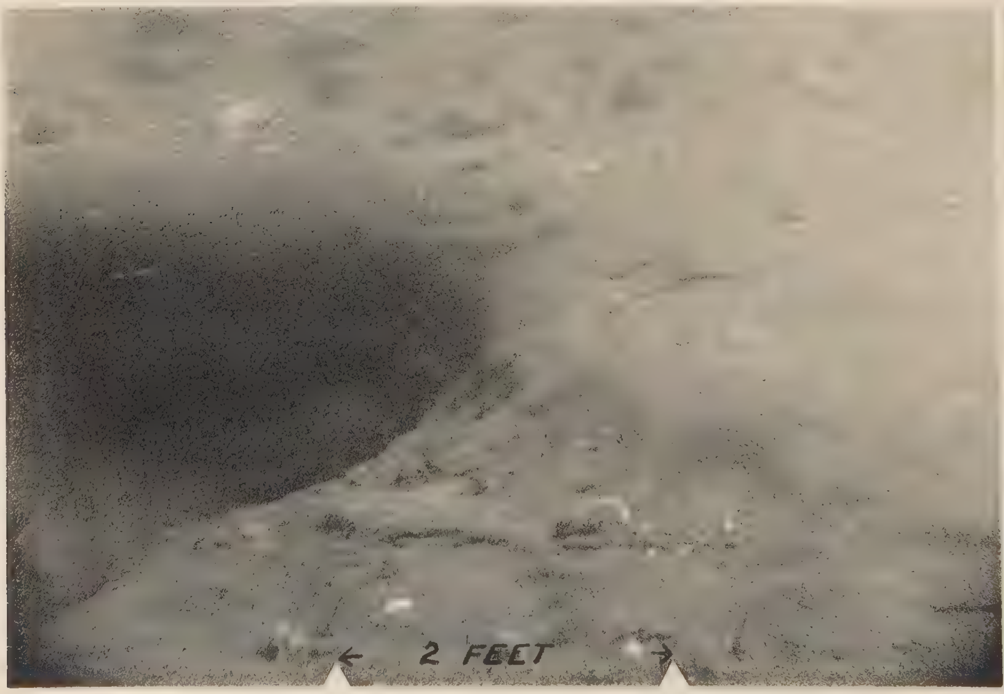

FIGURE 2. CLOSER VIEW OF HANGING VALLEY
Cobble-strewn floor of the valley above the 5-foot drop shown in background. Depth 65 feet. Location at H, Pl. 8.

HANGING VALLEY IN SEA LION GULCH

trasts between the land canyons north of La Jolla and those of the sea floor. The land canyons have extremely narrow notches at their base just wide enough for a man to squeeze through. These have not yet been reported from the two principal La Jolla submarine canyons, although some of the tributary valleys are almost as narrow and have equally steep walls. The alluvial cliffs in the land canyons are very much fluted by erosion developing columnar structure. Such fluting has not been found on the ocean bottom.

Some of the tributaries of the Grand Canyon show a remarkable resemblance to the head of Scripps Canyon. Fig. 2 of Plate 14 shows such tributaries, an inner gorge with abrupt change in slope at the rim, and vertical walls extending down to the bottom. If this land gorge were submerged and sediment allowed to accumulate in it, a flat floor similar to that in the submarine canyon might develop.

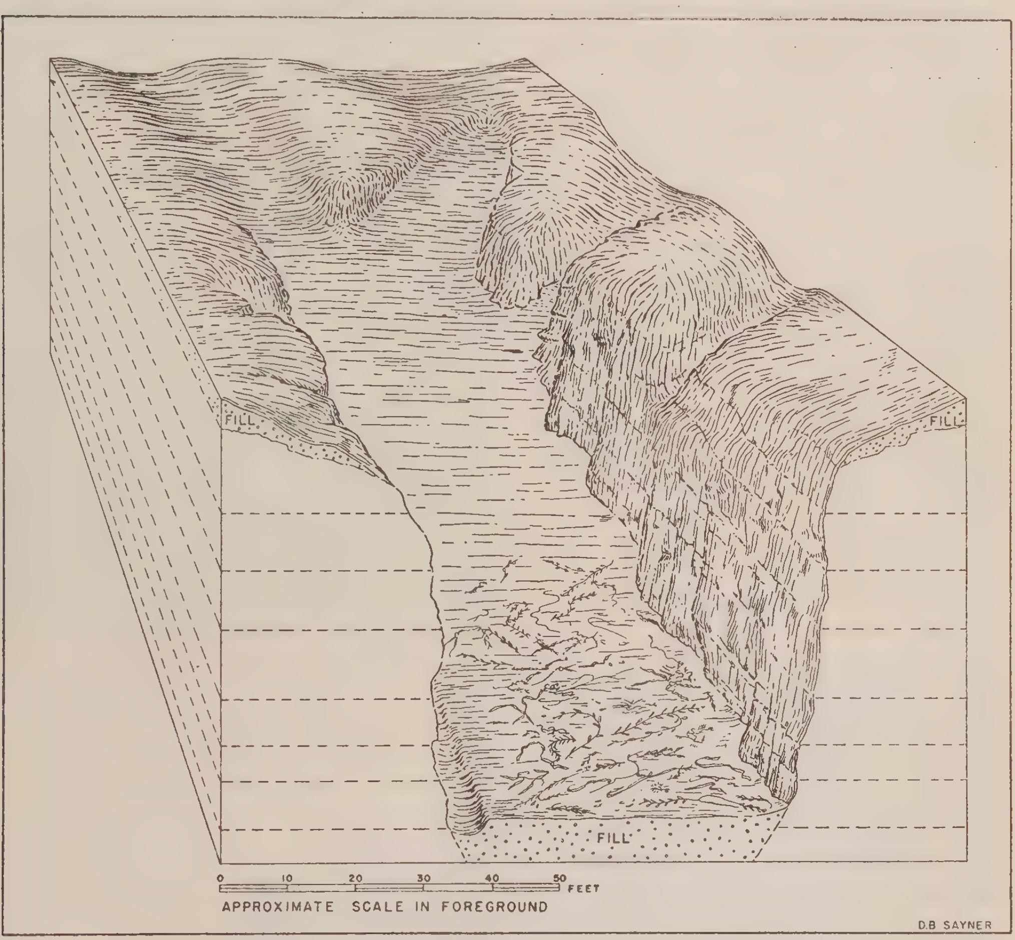

FIGURE 2.—BLOCK DIAGRAMS OF HEAD OF SUMNER BRANCH
The various features described for the dives in Sumner Canyon are illustrated. No vertical exaggeration intended. Diagram constructed by D. B. Sayner.

ORIGIN OF THE LA JOLLA CANYON HEADS

Suspension (Density) Currents

So much has been written showing how out of line with the facts are the hypotheses of canyon origin by faulting, by tsunamis, and by artesian spring sapping[4] that it seems unnecessary to repeat these as yet unanswered discussions. Certainly none of the features discovered by the diving operations support these interesting but unsatisfying hypotheses. Density currents, more properly called suspension currents, are still credited by a considerable number of scientists with at least contributing to an important degree to canyon origin. The fact has always been overlooked that the suspension currents which are so clearly developed in reservoirs are quite powerless to prevent deposition of fine material at the points where they should be most capable of cutting gorges. Kuenen (1947) recently attempted to apply the hypothesis to the La Jolla canyons. Unlike Daly (1936), Kuenen considers that the suspension currents are still in operation and thus can extend the canyons into the present shore. Since almost all the canyons (except those off the east coast of the United States) extend in to shoaler depths than those of the −40 to −60 meter level which Daly assumed existed during the time of canyon excavation, Kuenen's modifications would seem to be essential to bolster this hypothesis. Kuenen considered that canyons could be cut by the density flows provided they lacked sharp turnings and waterfall steps along the course of the canyons.

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[4] Points cited are as follows:
Against faulting, Shepard and Emery, 1941, p. 110–11.
Against tsunamis, Kuenen, 1947, p. 45; Shepard

The diving operations provide new direct evidence. Nothing reported by Haymaker indicated that suspension currents have had anything to do with the La Jolla canyons. The sharp turns and waterfall steps thought by Kuenen to be contrary to the hypothesis are definitely established by Haymaker's pictures and observations. Unfortunately for most of the diving operations, suspension currents failed to clear the canyons of the suspended mud which settled into them after being carried out from shore by rip currents. During the murkiest dives, when suspension currents should have been moving water down canyon, the currents showed an alternation of up- and down-canyon movement.[5] The fills on the canyon floors testify to the failure of suspension currents to keep the canyons clean at least under ordinary conditions. The cutting of vertical and overhanging cliffs consisting of rocks so compact that they were difficult to break is certainly not to be expected from suspension currents.

Mud Flow-Landslide Hypothesis

All recent writers have considered landsliding or mud flows along the ocean floor as an important process. Evidence of these mass movements is becoming well established from the studies of depth in the heads of the La Jolla canyons. The small trench in the fill of Sumner Branch (Pl. 3, fig. 2) might be considered evidence of a mud flow.

Could such movements produce deep elongate canyons with characteristics like those of the canyons off La Jolla? Given an appreciable slope at the edge of the continental shelf, what would happen if this inclined surface remained submerged over a long period of time? We can assume that much material would creep or slide down the slope and, if the underlying material were poorly consolidated, broad amphitheater-like indentations would develop. If the edge were underlain by well-consolidated rocks, as appears to be the case off La Jolla, changes should be so slow that millions of years would be required to produce any appreciable effects. Even if irregularities in the outer slope were developed, how could these turn into elongate narrow canyons with deep inner gorges and tributaries with patterns like those of the stream-cut canyons on the adjacent land? This difficulty has not yet been explained by those favoring the landslide hypothesis. Furthermore, the canyons apparently lack the basin depressions so common in landslide topography.

Excavation by Streams

The descriptions of the landward heads of the La Jolla submarine canyons and comparisons with adjacent land canyons seem to provide conclusive evidence that the process which formed the land canyons was also responsible for those on the sea floor. Such differences as exist are easily explained by sedimentation on the canyon floors and by the absence of rain wash on the canyon walls. After submergence, the extremely narrow gorges of the land canyons

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and Emery, 1941, p. 120–21; Shepard, 1948a, p. 59, 60, 240, 241.

Against artesian spring sapping, Rich, 1941; Daly, 1942; Kuenen, 1947, p. 43–44; Shepard and Emery, 1941, p. 115–116.

[5] In dives at the head of Monterey Canyon, where the water is very muddy, weak alternating currents were also reported by Haymaker.

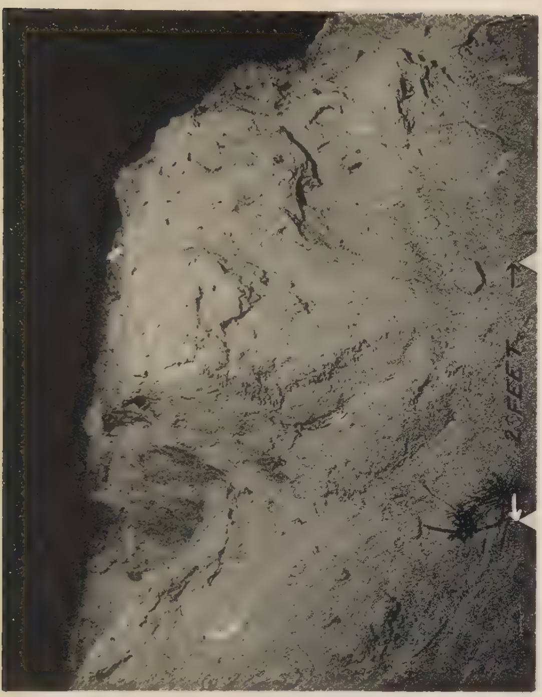

FIGURE 1. VERTICAL WALL OF ALLUVIUM IN LOWER PART OF PHANTOM DIKE GULCH
Note fish (Coryphopterus nicholsii) protruding from holes in the alluvium. Depth 100 feet. Location at K, Pl. 8.

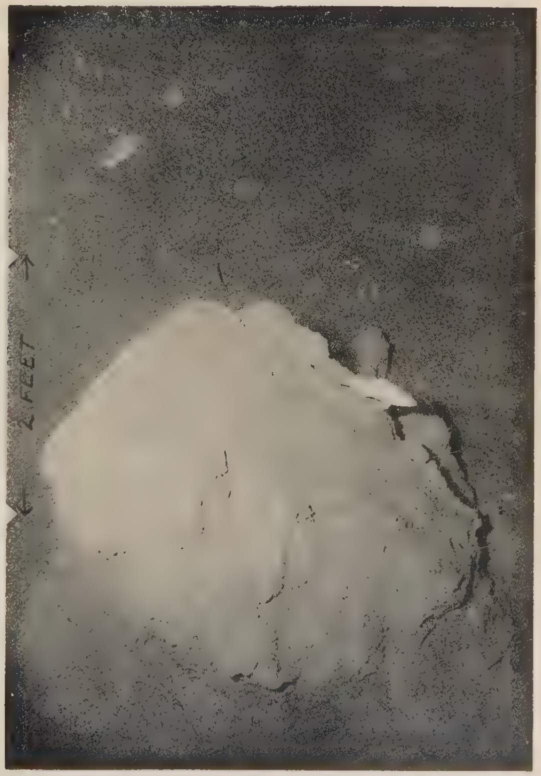

FIGURE 2. LARGE LUMP OF CLAY AT MOUTH OF PHANTOM DIKE GULCH
Found at point where gulch entered wide portion of main canyon. Fish are kelp bass (Paralabrax clathratus). Depth 130 feet. Location at L, Pl. 8.

VERTICAL ALLUVIAL CLIFF AND LARGE CLAY LUMP, IN LOWER PHANTOM DIKE GULCH

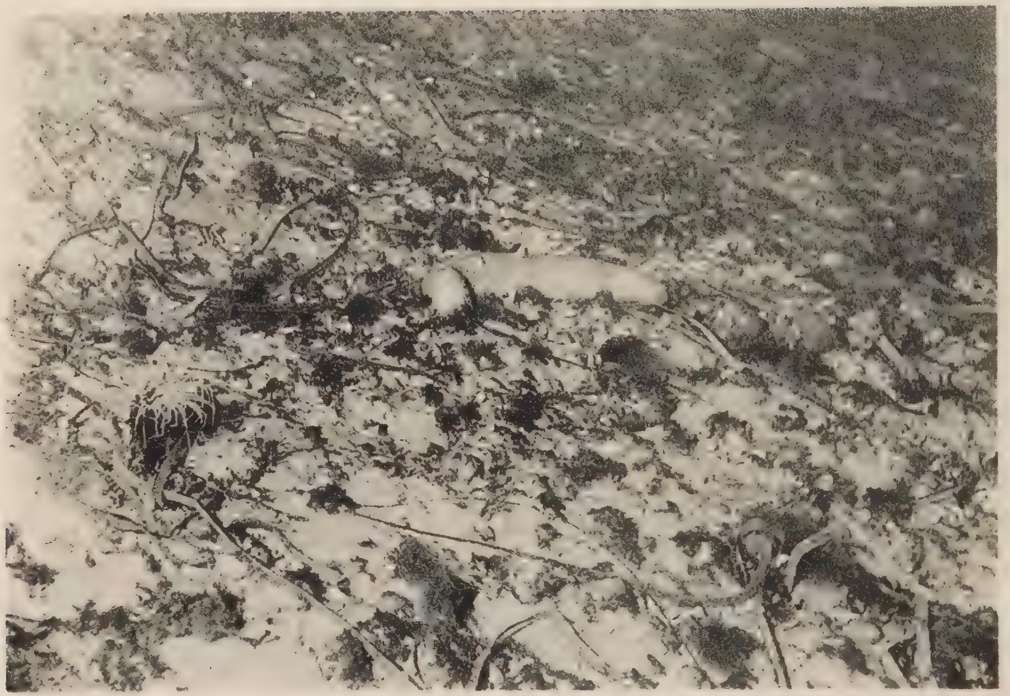

FIGURE 1. RIDGE WEST OF PHANTOM DIKE GULCH

Note abundance of life, including large holothurian and sea anemone, and the cobbles mixed in with the sand and kelp stalks. Good lighting in background comes from sunlight. Depth 58 feet. Location at M, Pl. 8.

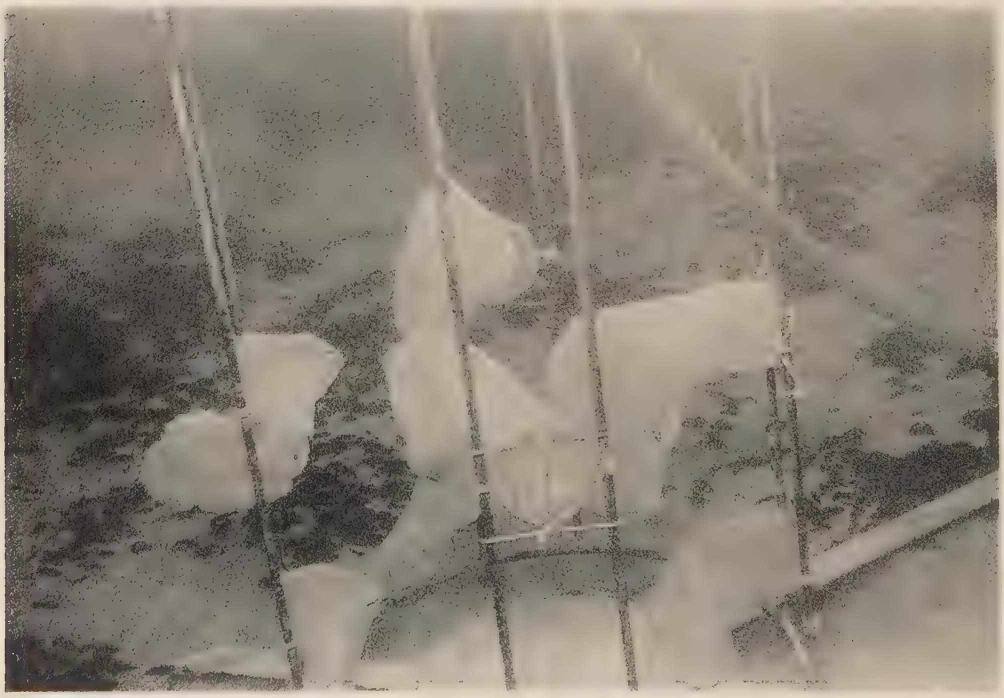

FIGURE 2. NEW TYPE OF SEDIMENT TRAP IN HEAD OF LA JOLLA CANYON

Socks caught more sand coming from the down-canyon side than from the up-canyon direction. Depth 50 feet. Location at N, Pl. 8.

RIDGE BETWEEN GULLIES NEAR PHANTOM DIKE GULCH AND SEDIMENT TRAP IN HEAD OF LA JOLLA CANYON

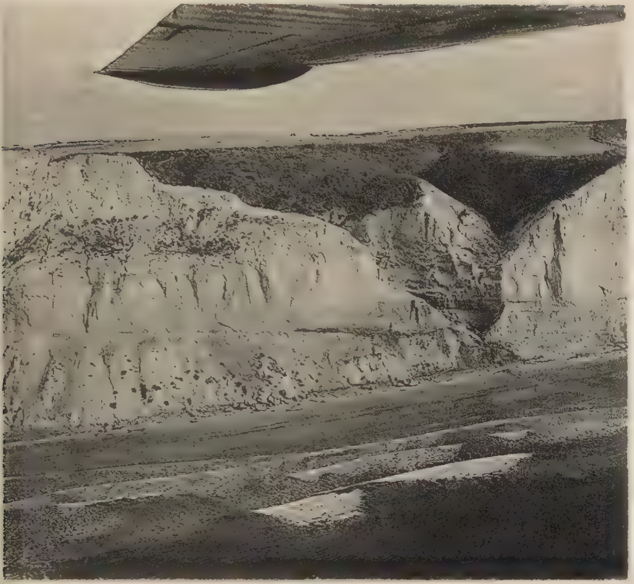

FIGURE 1. AIRPLANE VIEW OF GLIDER CANYON CUT INTO SEA CLIFFS NORTH OF HEAD OF SCRIPPS CANYON
Note hanging tributary.

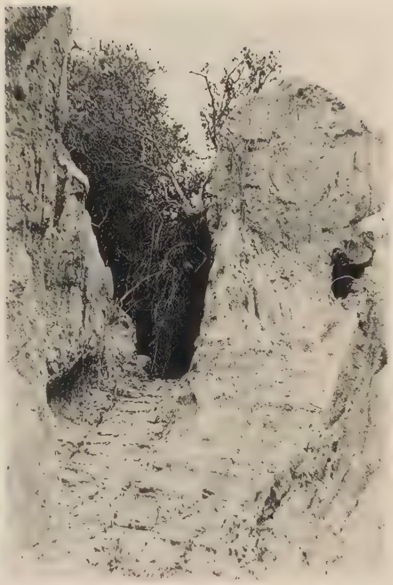

FIGURE 2. HANGING VALLEY ON LAND CUT IN ALLUVIUM
It is comparable to the hanging valley of Sea Lion Gulch shown in Plate 10.

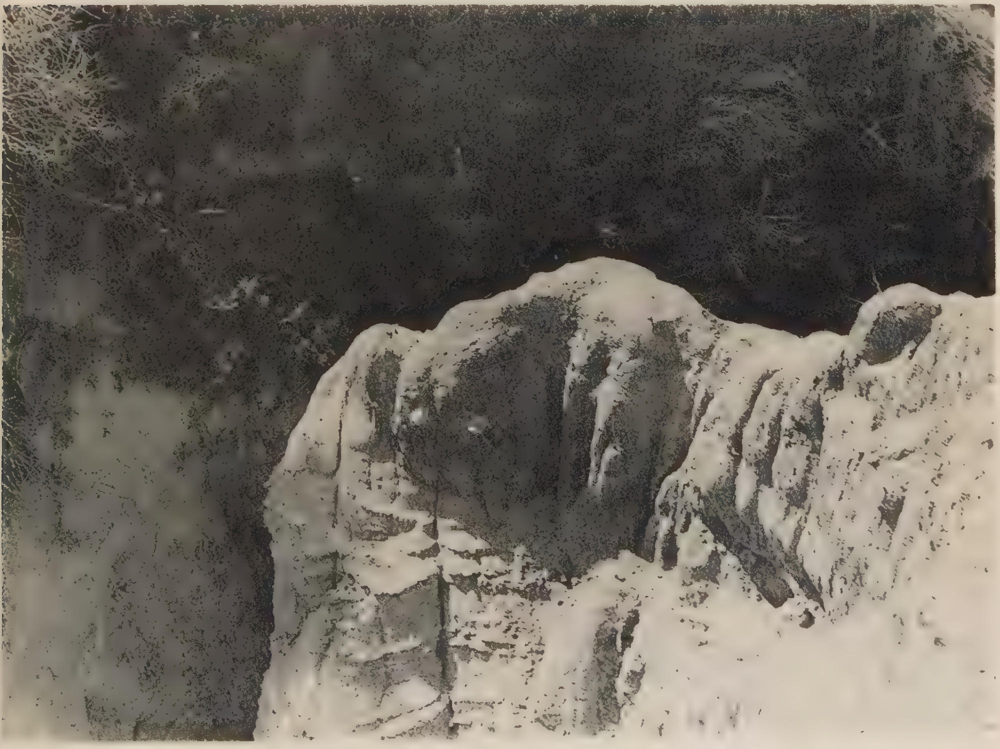

FIGURE 3. SHOULDER IN ALLUVIUM AT HEAD OF CANYON CUT IN CLIFFS NORTH OF SCRIPPS INSTITUTION
Compare a similar feature on the sea floor shown in Pl. 9, fig. 2.

FEATURES OF LAND CANYONS ADJACENT TO SCRIPPS CANYON

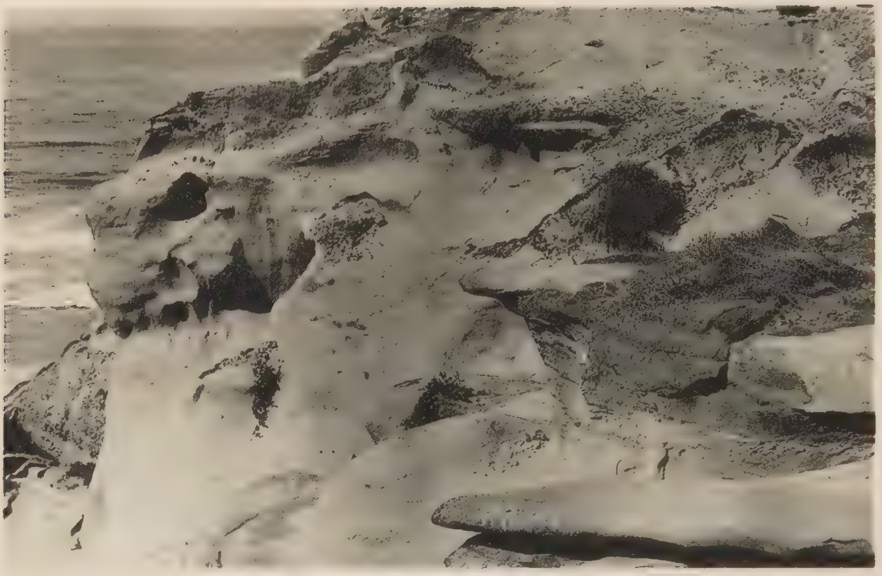

Figure 1. Vertical North Wall of Glider Canyon
Note projecting ledges which are comparable to Pl. 3, fig. 4.

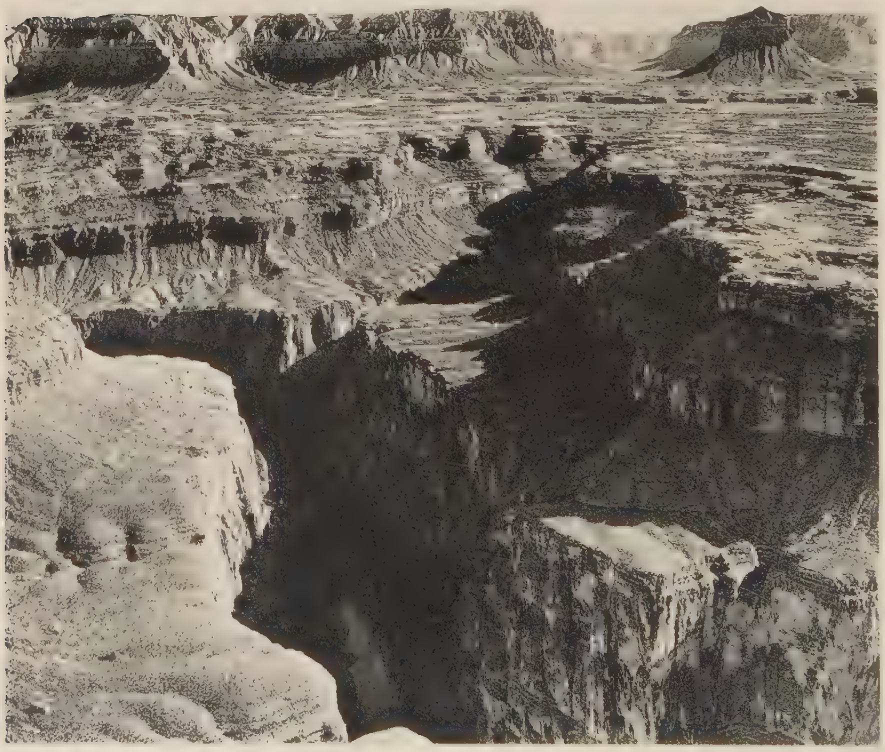

Figure 2. Tributary to Grand Canyon which Appears to be Similar to Head of Sumner Branch
Compare Figure 2. Airplane photo by Robert S. Dietz.

LAND CANYON AT LA JOLLA AND TRIBUTARY OF GRAND CANYON would quickly fill with sediment, and this fill would be held in place by the walls. The fluting and columns of the alluvial land cliffs would tend to disappear after submergence. As submarine weathering proceeded, these features, which are due to running water, would not appear unless density currents of the type predicted by Daly and Kuenen were flowing over the sides.

Clearly, the major characteristics of the La Jolla marine canyons are those of the adjacent land canyons. The evidence that land canyons are the result of stream erosion is so conclusive that few geologists deny it. Unless oceanographers and marine geologists have overlooked some important process, it seems only reasonable to assume that the canyons which Haymaker has photographed on the sea floor off La Jolla were excavated by streams when the sea was lower or the land higher.

SIGNIFICANCE OF THE LA JOLLA CANYON INVESTIGATIONS

A prominent geologist, after hearing of the evidence from the dives relative to the canyon heads, asked why it was significant since it was well known that the sea stood several hundred feet lower during the glacial stages, so that the excavation described could have been due to a moderate lowering. The answer to this good question is that lowering of a few hundred feet would expose the continental shelves which have gentler slopes off most places, including La Jolla, than the adjacent land. As a result these gentle slopes would become covered by fans rather than truncated by narrow gorges. One can easily imagine the result of exposing an undissected shelf off the sea cliffs shown in Plate 2. Every flood would help the construction of fans on the emerged sea floor. Canyons like those off La Jolla would be cut only at places where the lowered sea level exposed steep slopes or steep valley heads formerly covered by the sea.

Furthermore, if cliffs without canyons had been exposed by a 40–60 meter lowering of sea level the new gorges would necessarily terminate at that sea level, just as the canyons in the marine cliffs north of Scripps Institution today terminate near the present sea level. A study of the charts of the world shows no such canyons along any coast.[6] Canyons like those at La Jolla give no indication of sudden change in character at 40–60 meters below sea level nor, for that matter, at much greater depths. The close approach of the canyon heads to the shore at La Jolla is nothing unusual and is found in scores of other places around the world. Nor does the La Jolla area show any indication of recent diastrophic activity. Broad wave-cut terraces are in accord with present sea level (Shepard, 1948a, Fig. 60). A continental shelf of approximately normal depth lies off the coast everywhere in the La Jolla area except where cut by submarine canyons.

POSSIBLE SEQUENCE IN DEVELOPMENT OF LA JOLLA CANYONS

Primary Deep Excavation

Despite the objections raised by some geologists to the idea that the continental borders once stood much higher than they do at present (or that the sea was formerly much lower) submarine geological operations and almost all surveys of the sea floor continue to supply evidence which is extremely difficult to interpret except by invoking major changes of level (summarized in Shepard, 1948a, p. 241–248, 332–335; 1948b). In addition to the river-canyon topography of the sea floor, the finding of rounded cobbles, flat-topped sea mounts, terraces, and shallow-water shells in water hundreds of fathoms deep strongly indicates submergence. The borings and geophysical prospecting of coral reefs have all yielded evidence which is convincing to most geologists that the coral-reef areas have undergone great submergence (Kuenen, 1947; Ladd *et al.*, 1948). We need not discuss here whether the world-wide changes indicated by these interlocking lines of evidence mean that the sea stood lower at one time or the continental margins, oceanic islands, and sea mounts stood higher, nor is it necessary to consider whether the changes took place at one time or at several times. The important point seems to be that, unless all this evidence is void, coasts have formerly stood relatively much higher than they do now. The evidence for southern California is particularly complete (Shepard and Emery, 1941). Therefore, it is by no means unreasonable to assume that at some time, possibly in the very late Tertiary[7] or in the Pleistocene, not only the shelf but the steep upper slopes of the San Diego Trough off La Jolla were above water. At such a time canyons would have been cut into these exposed slopes. This canyon cutting must have been of relatively short duration, unless the narrow gorges of Scripps Canyon and of parts of La Jolla Canyon represent a development more recent than that of the main canyons.

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[6] Shallow sea valleys with gentle gradients and gentle wall slopes like that off the Hudson should not be confused with submarine canyons.

Drowning of Canyons

If we assume further that the sea or the land returned more or less to its present level, the sediments washed out from the lands would have tended to fill the canyon heads. However, in places where the canyon gradients were relatively steep or where the sediment was sufficiently mobile, the canyons would have been maintained by occasional mud flows or landslides. Elsewhere, the rapidly shifting sands would have soon obliterated the canyon heads. The outer portions of the canyons may have been filled by the very mud flows which were maintaining the inner portions, although it is equally possible that the mud in the flows went into suspension and was ultimately deposited as a thin blanket in San Diego Trough.

Accompanying the filling of canyon heads, there would have been straightening of the coasts by a combination of estuary filling and sea-cliff cutting into the projecting headlands.

Shifting Sea Levels of the Glacial Stages

If the major cutting of the canyons had preceded some or all of the glacial stages, the swinging sea levels of the Pleistocene would have had a very different effect on the dissected continental shelf than on a smooth shelf. The lowered sea levels would have laid bare the steeply sloping inner portions of the unfilled canyons, and as a result erosion would have taken place at the canyons heads. At the same time alluvium was forming on the inner shelf but eventually the headward erosion of the canyon would have cut through this alluvium. The forming of the alluvial-walled gullies at the head of La Jolla Canyon could thus be explained as the product of this glacial-stage erosion. Because the last rise in sea level at the end of the Wisconsin took place only 10,000 to 25,000 years ago, it is not surprising that these alluvial walls should be still well preserved. The vertical walls at the head of Scripps Canyon may also be quite recent or at least recently re-excavated.

It is evident that the headward erosion during the glacial stages of lowered sea level did not cut the present land canyons below the present sea level (Pl. 2). The absence of estuaries or filled estuaries may prove puzzling to some readers, particularly in view of the existence of the high gradients at the canyon heads at a distance of about 900 feet from the cliff. In view of the present slow rate of rock-cliff retreat in the area (Shepard and Grant, 1947), probably not more than a foot per century, the present cliffs have probably not retreated very far in the few thousand years since the last rise in sea level. Assuming the existence of the sea cliffs and the land canyons during the last glacial lowering, it can be further assumed that deposition would take place on the exposed shelf, particularly at the canyon mouths. The fans formed as a result of this deposition would cause the spreading into distributaries of the occasional flood waters emerging from the present land canyons and would thus have prevented the concentration of water into the unfilled heads of the exposed submarine canyons. Furthermore, the headward erosion in the exposed canyon heads would have been somewhat counteracted by the fan deposition at the mouths of the present land canyons. As a result, retreat may not have been very great during the time the canyon heads were exposed.

Maintenance of the Canyon Heads at the Present Day

Studies of sand movements along the shore show that there is enough shifting of sediment to allow the filling of the canyon heads, as they now exist, in a few decades. Also, shoaling found at the canyon heads during certain periods demonstrates that the canyons are receiving this sediment. Since the canyons are not filled, processes must exist which are keeping them clean. The existence of mud flows is well demonstrated for the La Jolla canyons by the deepening which has been found on two occasions at the canyon heads. The small trench in the filled bottom of Sumner Branch (Pl. 3, fig. 2) is also particularly impressive. The La Jolla canyons have an abundance of kelp and eel grass within the fill, and this mixed with mud and sand should provide good sliding material in view of the steep bottom gradients.

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[7] The canyons of southern California cut Miocene rocks in several places, and Monterey Canyon cuts a Pliocene formation.

Summary and Conclusions

Diving operations into the heads of the La Jolla submarine canyons have yielded new information regarding the details of these marine features. The telephonic descriptions during the course of the dives and the submarine photographs leave little doubt as to the exact character of the walls and the floors of the canyon. Scripps Canyon and its main tributary were found to be cut into firm Eocene conglomerate, sandstone, and limestone, and to have steep upper slopes and a vertical-walled inner gorge. Numerous gullies cut the vertical wall, some of them as hanging valleys and others as steeply descending accordant tributaries. Except for the thick cover of sediment on the steeply sloping canyon floor, Scripps Canyon appears to be remarkably similar to the canyons cut into the terrace and sea cliffs on the adjacent land.

The head of La Jolla Canyon is characterized by a network of tributaries which are excavated out of an alluvial formation similar to alluvium on the near-by land. These tributaries have high gradients and are characterized by their precipitous side walls. Some of the walls contain large masses of cobbles. Only one rock outcrop was encountered during the dives, although it is known that La Jolla Canyon has rock at somewhat greater depths. A hanging valley or a waterfall step was seen along the course of one tributary. The head of La Jolla Canyon has features which are almost exactly duplicated by the cuts in alluvium in the canyons north of Scripps Institution.

The floors of all the canyons had a cover of sediment. In the upper portions this sediment was sand, but beyond about 40- or 50-foot depths a considerable admixture of mud was encountered and decaying eel grass and kelp were abundant in most places. At the greatest depths there was less kelp, and the sediment was largely sand. In a few places cobbles were encountered on the valley floors.

The characteristics of these La Jolla marine canyons seem to leave little doubt of their stream origin. No submarine currents capable of excavation were encountered, nor were there ripples on the floors of the canyons except in a few places in very shallow water where wave oscillation was obviously responsible. New evidence was obtained that mud flows or landslides are operating to prevent the complete filling of the canyon heads. The hypothesis is proposed that the canyons were excavated at a relatively remote time and have undergone subsequent modifications in response to glacially controlled changes in sea level.

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THE OCCURRENCE AND CHARACTERISTICS OF METHANE-OXIDIZING BACTERIA IN MARINE SEDIMENTS[1]

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The chemical stability of methane, its common occurrence in the biosphere, and its importance in the petroleum industry have aroused considerable interest in the microorganisms that decompose this gas. There have been very few contributions to the study of such microorganisms since Kaserer (1905) and Söhngen (1906, 1910) almost simultaneously reported the bacterial oxidation of methane, and Münz (1915) investigated the physiology of a methane-oxidizing bacterium.

The widespread occurrence of methane-oxidizing bacteria in Italian soils was reported by Giglioli and Masoni (1914). These workers, like Harrison and Aiyer (1914, 1916*a*,*b*) and Aiyer (1920), who investigated methane oxidizers in Indian swamp rice soils, emphasized the importance of such bacteria in the conservation of carbon and in the formation of organic matter. From soil, Hasemann (1927) isolated bacteria which oxidized illuminating gas. Tausz and Donath (1930) isolated from soil a bacterium that was able to oxidize methane and also hydrogen, ethane, propane, butane, and higher hydrocarbons.

Based upon the presence or activities of bacteria that oxidize methane in surface soil overburdening subterranean gas or oil deposits are the so-called geomicrobiological prospecting methods (ZoBell, 1946*b*). Yurovskii *et al.* (1939) reported that in preliminary field tests up to 96 per cent of the methane in the atmosphere of coal mines was destroyed by strategically located cultures of *Methanomonas methanica*. Peroxidase formation by methane-oxidizing bacteria has been reported by Slavnina (1947), who also noted that, unlike allied species that oxidize higher hydrocarbons, *M. methanica* exhibited no fluorescence (Slavnina, 1948).

Although apparently occurring quite commonly in soil, particularly in regions where much methane is formed or found, methane-oxidizing bacteria are still regarded more or less as biological curiosities. These investigations were undertaken in view of the restricted body of data available on the physiology and morphology of methane-oxidizing bacteria and an almost complete lack of knowledge regarding their occurrence in marine materials.

MATERIALS AND METHODS

A modified Söhngen culture apparatus (figure 1) was employed for demonstrating and following the activity of methane-oxidizing bacteria. All-glass apparatus proved to be no better than 180-ml prescription bottles fitted with two-hole rubber stoppers. Although there are several ways of manipulating the apparatus, one of the best was to introduce the inoculum and the gas mixture in the culture bottle (A, figure 1) and fill the reservoir bottle (B) with sterile medium. Then by releasing the clamps (C, C′) 20 ml of medium were permitted to flow from the reservoir bottle into the culture bottle, after which the clamp on the culture bottle was securely closed and that on the reservoir bottle left open. As methane and oxygen were consumed in the culture bottle more medium was sucked over from the reservoir bottle. Graduation marks on the bottles provided for reading, at constant temperature and corrected atmospheric pressure, the volumes to ±0.5 ml. In this way gas uptake could be followed from day to day without interrupting the experiment.

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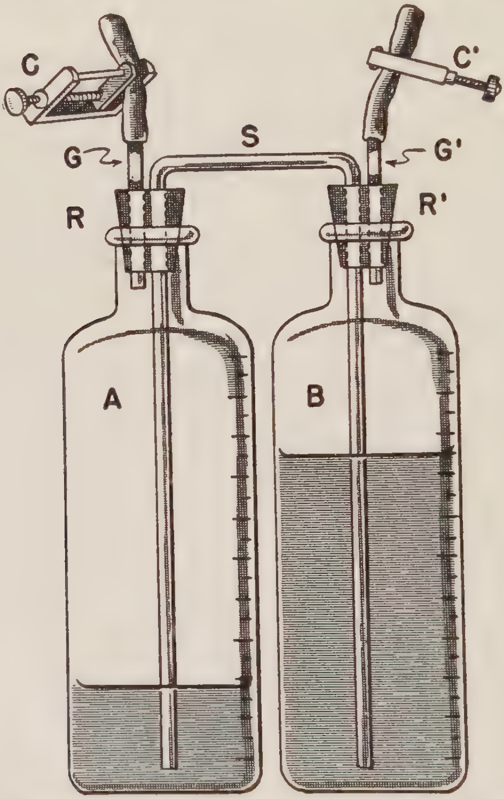

Figure 1. Modified Söhngen apparatus employed for studying respiration of methane-oxidizing bacteria. A, culture bottle; B, reservoir bottle; C, clamps on rubber tubing; G, glass inlet tubes plugged with cotton; R, two-hole rubber stoppers, S, glass siphon.

At the end of the experiment the residual gas in the culture bottle was transferred over mercury to a Fisher unitized precision model Orsat type gas analyzer (Matuszak, 1934). The apparatus provided for determining methane with an accuracy of ±0.4 per cent and oxygen and carbon dioxide somewhat more precisely. Gases of highest obtainable purity were employed for preparing the mixtures of methane, oxygen, carbon dioxide, and nitrogen.

Sea water aged to minimize its organic content (ZoBell and Grant, 1943) or a balanced mineral salts solution was employed in the preparation of the media. The nitrogen requirements were satisfied by ammonium salts, nitrate, or certain amino acids.

In the isolation and characterization of pure cultures, culture tubes or petri dishes were incubated in vacuum desiccators filled with the desired gas mixtures. Washed agar or silica gel was employed to prepare solid media.

DISTRIBUTION OF METHANE OXIDIZERS

Sediment samples from numerous regions have been tested for the presence of methane-oxidizing bacteria. In making the ecological survey, approximately one gram of material (wet weight) was used as an inoculum. Preliminary experiments indicated that, when such bacteria were present in a given environment, nearly all one-gram samples produced positive results, although a longer incubation period might be required than when 10- or 50-gram inocula were used. Actually 0.1-gram samples of marine mud often yielded positive results, and methane oxidizers were demonstrated in some 0.01-gram samples after several weeks' incubation in sea water medium enriched with methane. Such bacteria were not detected in surface sea water even when 100-ml samples were used as inocula.

TABLE 1

Number of samples tested in which methane-oxidizing bacteria were detected in one-gram inocula

DESCRIPTION OF MATERIAL	TOTAL NUMBER OF SAMPLES TESTED	NUMBER SHOWING PRESENCE OF METHANE OXIDIZERS
Surface samples (topmost 10 cm)		
Marine mud	21	18
Brackish water mud	41	36
Paraffin earth	9	9
Oil- or gas-field soil	187	139
Beach sand	9	2
Subsurface samples (below 10 cm)		
Marine mud	17	4
Brackish water mud	12	1
Beach sand	3	0

Since the samples were not collected or examined simultaneously, the results are not strictly comparable. Some samples collected far at sea were stored in a refrigerator at near 0 C until they could be examined in the laboratory. Therefore results are recorded as positive and negative only. Negative results may not establish the complete absence of methane-oxidizing bacteria because they may have perished or failed to multiply under the experimental conditions to which they were subjected, but complete reliance can be placed upon positive results.

Methane-oxidizing bacteria were found in marine sediments collected off the coast of California, in the Gulf of Mexico, in the Atlantic Ocean off the coast of New Jersey and Massachusetts, in brackish water sediments from California and Louisiana, and in surface soil from oil and gas fields in California, Louisiana, Oklahoma, and Texas (table 1).

With very few exceptions methane-oxidizing bacteria were not detected in subsurfaces mud samples collected at core depths exceeding 10 cm, presumably because free oxygen becomes a limiting factor at such depths. Not only is free oxygen nearly always absent below the topmost few millimeters of marine mud, but negative redox potentials generally prevail (ZoBell, 1946*a*). In arid soil penetrated by oxygen methane-oxidizing bacteria have been found at depths of several feet.

Finding methane-oxidizing bacteria in marine mud under 1,170 meters of water where the hydrostatic pressure is approximately 117 atmospheres indicates that such pressures do not limit the activities of these bacteria. In fact, experiments now in progress suggest that much higher hydrostatic pressures may actually enhance the activity of barophilic (ZoBell and Johnson, 1949) methane oxidizers from oceanic deeps.

ISOLATION OF PURE CULTURES

After 5 to 14 days' incubation in an atmosphere containing methane, oxygen, and carbon dioxide, enrichment cultures were streaked on solid media. Although many colonies developed, most of them failed to utilize methane when transferred back to Söhngen culture bottles containing methane, oxygen, and carbon dioxide. Serial transfers of the enrichment cultures yielded on solid media colonies that definitely utilized methane when transplanted to appropriate liquid media.

Out of 82 colonies picked from washed agar medium only two proved to be methane oxidizers. Many more colonies developed on nutrient agar (0.5 per cent peptone and 0.3 per cent yeast extract), but none of them consumed methane when transplanted to Söhngen culture bottles. Growth was rather sparse on silica gel plates even when the inoculum was large, but out of 68 colonies picked from this purely mineral medium 12 showed ability to consume methane.

Cultures of methane oxidizers, which proved to be pure according to all standard criteria, including both cultural and microscopic tests, formed discrete colonies 0.1 to 0.5 mm in diameter. The colonies were pearly or bronzy in appearance, convex, and circular with an entire margin. Other colonies of methane oxidizers subsequently isolated proved to have similar characteristics, although two other colonial types, which did not utilize methane, often developed from enrichment cultures.

CHARACTERISTICS OF PURE CULTURES

Morphologically all methane-oxidizing bacteria isolated from marine mud or soil were similar. The organisms are gram-negative, nonsporeforming rods with rounded ends, ranging in diameter from 0.6 to 1.0 micron and in length from 2.0 to 3.3 microns. The rods frequently showed lightly stained areas when stained with 3 per cent nigrosine, suggesting vacuolation.

Establishing that in the early stages of their life cycle the methane oxidizers are motile by means of one or more polar flagella required much patience and perseverance. The difficulty was in finding young cells for examination because from 5 to 20 days' incubation are required for the cultures to develop turbidity in liquid media or macroscopically visible growth on solid media. By this time most of the cells are nonmotile.

In older cultures the bacteria produced a melanoid pigment, eventually forming a chocolate-colored growth, echinulate at the bottom of the stroke and becoming beaded on top of potassium nitrate agar slants in the presence of an atmosphere of methane, oxygen, and carbon dioxide. When streaked on plates of such medium the bacteria formed colonies of the type described above. After 5 days' incubation at 27 C the colonies were fluid and, with further incubation, gradually became sticky and brownish in color. Deep colonies were biconvex, lens-shaped, and brown in color after 20 days. They failed to grow on nutrient agar, broth, or gelatin in the absence of gaseous hydrocarbons. (Either methane, ethane, or propane supported the growth of the bacteria in the presence of oxygen and carbon dioxide.)

In the presence of appropriate mixtures of methane, oxygen, and carbon dioxide the methane oxidizers started to render liquid medium cloudy after 4 to 10 days' incubation at 27 C. A delicate pellicle sometimes appeared in the later stages of growth. After 2 or 3 weeks the medium became less turbid and a clumpy sediment formed on the bottom of the culture vessel. In active cultures gas uptake became apparent within a day or two and continued for 2 or 3 weeks.

Ammonium salts, nitrate, glutamic acid, or peptone served as nitrogen sources. Glycine was not utilized. Certain strains of methane-oxidizing bacteria oxidized ammonia to nitrite, an observation of special significance which will be elaborated elsewhere.

The methane-oxidizing bacteria studied by Söhngen (1906), Münz (1915), Aiyer (1920), Hasemann (1927), and Tausz and Donath (1930) are too inadequately described to permit detailed comparison with our pure cultures. The latter differ from *Methanomonas methanica* (Söhngen) Orla-Jensen (Breed *et al.*, 1948) in at least two respects: the growth of *M. methanica* is described as membranous whereas all of our methane oxidizers produced a turbid growth in liquid medium and, unlike our cultures, *M. methanica* required for its growth the initial presence of no more carbon dioxide than is normally present in the atmosphere. Also unlike our methane-oxidizing bacteria the culture of Münz (1915) readily utilized as energy sources acetate, butyrate, tartrate, glycerol, mannitol, glucose, sucrose, and peptone. These and other minor differences suggest the likelihood of two or more different species being involved, a subject which will be treated separately.

It is still problematical how many bacterial species are able to oxidize methane, though certainly more than one. In this connection it is of interest to point out that considerably more than 100 microbial species representing nearly 40 genera have been shown to be able to attack higher hydrocarbons (ZoBell, 1946*b*). The methane oxidizer of Münz (1915) was said to utilize neither ethane nor ethylene, but the "methane bacterium" of Tausz and Donath (1930) allegedly oxidized hydrogen, ethane, propane, butane, and higher paraffin hydrocarbons as well as methane. Slavnina's (1948) culture, like some of ours, utilized methane, ethane, and propane. Störmer's (1908) *Bacillus hexacarbovorum*, which utilized toluene and xylene, could also assimilate methane.

FACTORS AFFECTING METHANE OXIDATION

Oxygen tension. In order to evaluate the influence of oxygen tension on the growth and activity of methane-oxidizing bacteria, gas mixtures were prepared consisting of 20 per cent methane, 10 per cent carbon dioxide, and from 0 to 70 per cent oxygen. Nitrogen was employed as an inert diluent, when necessary, to bring the partial pressure up to 100 per cent, after having established that it was neither fixed nor evolved. Söhngen culture bottles inoculated with 1.0 ml of strain 37:146-1 were filled with the various gas mixtures and 20 ml of NH_4Cl mineral solution, thereby leaving approximately 150 ml of gas in each bottle at the beginning of the experiment. The cultures were incubated for 6 days at 32 C after which the gas volumes were measured and analyzed. Representative data from one experiment are summarized in table 2.

TABLE 2

Average amount of methane consumed per day by methane-oxidizing bacteria during 6 days at 32 C in an atmosphere initially containing 20 per cent methane, 10 per cent carbon dioxide, and varying partial pressures of oxygen and nitrogen

PARTIAL PRESSURE OF		METHANE CONSUMED PER DAY BY	
Oxygen	Nitrogen	A	B
%	%	*ml*	*ml*
0	70	0.00	0.00
10	60	1.05	0.94
20	50	0.88	0.88
30	40	1.05	1.05
40	30	—	0.94
60	10	0.35	0.52
70	0	0.23	0.29

From such experiments the dependence of methane oxidizers upon free oxygen was established. As the oxygen partial pressure increased from 0 to 10 per cent the rate of methane consumption increased. Within the limits of experimental error methane consumption was about the same between oxygen partial pressures of 10 and 40 per cent. Increasing the oxygen partial pressure above 40 per cent resulted in a decreased rate of methane consumption. This latter observation is in agreement with findings reported by ZoBell (1946*b*), but Münz (1915) obtained the best results with only 2 per cent oxygen.

Below 10 per cent oxygen partial pressure the rate of methane consumption appears to be independent of oxygen tension until reduced to such a low level that oxygen is consumed by bacteria faster than it can be replaced by diffusion. Shoup (1929) and ZoBell (1940) have observed a similar relationship between oxygen concentration and oxygen consumption by other bacteria. It should be obvious, however, that in spite of the influence of oxygen tension on microbial activity, oxidations dependent upon oxygen will stop when oxygen is depleted. Therefore, in order to provide for maximum activity over extended periods of time it is desirable to start with gas mixtures having the highest allowable oxygen partial pressure in closed systems. The same applies to methane partial pressures.

Methane partial pressure. The rate of methane oxidation was found to increase as the methane partial pressure was increased from 0 to 40 per cent, above which the rate was approximately the same within the limits of experimental error (table 3). In supplementary experiments it was found that methane partial pressures up to 95 per cent were well tolerated, but under these conditions oxygen and carbon dioxide become limiting factors. Similar observations were made by Münz (1915).

TABLE 3

Average amount of methane consumed per day by methane-oxidizing bacteria during 6 days at 32 C in an atmosphere initially containing 20 per cent oxygen, 10 per cent carbon dioxide, and varying partial pressures of methane and nitrogen

PARTIAL PRESSURE OF		METHANE CONSUMED PER DAY BY	
Methane	Nitrogen	A	B
%	%	*ml*	*ml*
0	70	0.00	0.00
10	60	0.33	0.40
20	50	1.00	1.00
30	40	—	0.94
40	30	1.80	1.80
60	10	1.74	—
70	0	1.86	2.04

Carbon dioxide requirements. Although there is enough carbon dioxide in ordinary air (0.03 per cent) to provide for the multiplication of some methane-oxidizing bacteria, the presence of from 5 to 10 per cent carbon dioxide in the initial gas mixture materially enhances multiplication and methane oxidation. Neither the carbonate nor the bicarbonate ion proved to be as satisfactory as free carbon dioxide for initiating the growth of methane oxidizers. Once they start to grow, from 40 to 90 per cent of the methane oxidized may be converted into carbon dioxide (table 4). Since the bacteria require carbon dioxide and utilize no carbon compound except gaseous hydrocarbons, carbon dioxide is believed to be converted into bacterial cell substances. A slight decrease in the rate of methane consumption occurred as the carbon dioxide partial pressure was increased from 20 to 30 per cent.

Oxidation-reduction potential. Experiments designed to determine the effect of initial oxidation-reduction potential on the activity of methane-oxidizing bacteria were complicated by the incompatibility of free oxygen, which is required by the bacteria, with reducing agents required to obtain low potentials. Sodium thioglycolate proved to be the most satisfactory reducing agent for reducing the redox potential in the presence of free oxygen. With it a series of mineral media were prepared having redox potentials ranging from E_h −46 to +322 mv at pH 6.6. The media were inoculated uniformly with culture 37:146-1 and incubated at 32 C in an atmosphere consisting initially by volume of 30 per cent methane, 60 per cent oxygen, and 10 per cent carbon dioxide. The E_h was determined with a platinum electrode and the pH with a glass electrode using a saturated calomel half cell with a Beckman meter. The values at the beginning of the experiment and after 10 days' incubation for a representative experiment are recorded in table 5 together with data on the amount of methane consumed.

TABLE 4

Methane and oxygen consumed and carbon dioxide produced by six different cultures of methane-oxidizing bacteria in 10 days at 30 C

CULTURE NUMBER	METHANE CONSUMED	OXYGEN CONSUMED	CARBON DIOXIDE PRODUCED
	ml	*ml*	*ml*
37:206- 1	14.0	24.1	8.9
2	19.7	39.6	8.2
3	18.8	39.3	7.9
6	4.1	8.0	3.0
9	7.0	12.8	5.7
10	13.8	29.3	8.1

TABLE 5

Effect of oxidation-reduction potential, expressed as E_h values at pH 6.6, of medium on the amount of methane consumed by methane-oxidizing bacteria during 10 days' incubation at 32 C

INITIAL E_h OF CULTURE		FINAL E_h OF CULTURE		METHANE CONSUMED BY CULTURE	
A	B	A	B	A	B
mv	*mv*	*mv*	*mv*	*ml*	*ml*
−46	−44	+75	+76	5	—
+72	+70	+297	+297	10	6
+95	+94	+281	+252	8	7
+226	+213	+278	+254	15	22
+322	+322	+335	+361	45	46

Although certain anomalies appeared in this and similar experiments, it is clear that methane oxidation is favored by higher potentials. It is doubtful that methane-oxidizing bacteria are active in media having negative E_h values at pH 6 to 8.

Effect of pH. The effect of pH on the activity of methane-oxidizing bacteria is illustrated by the data in figure 2. Balanced mineral salts solutions enriched with KNO_3 as a nitrogen source and 0.3 M phosphate buffers were prepared having initial pH values ranging from 4.5 to 8.3 when in equilibrium with an atmosphere containing by volume 10 per cent carbon dioxide, 30 per cent methane, and 60 per cent oxygen. The media were incubated at 27 C after being inoculated with 1.0 ml of an active liquid culture of methane-oxidizing bacteria.

Although culture 37:146-1 exhibited maximum methane consumption at around pH 6.5 and no activity above pH 8.0 under these experimental conditions, methane oxidation by other cultures has been demonstrated in medium as alkaline as pH 8.8. Large numbers of methane-oxidizing bacteria have been found in marine sediments, the pH of which ranges from 6.4 to 9.5 (ZoBell, 1946*a*).

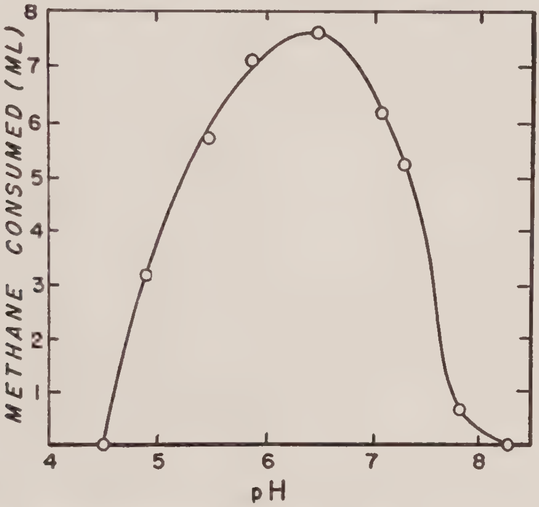

Figure 2. Amounts of methane consumed in 42 days at 27 C by methane-oxidizing bacteria in media of different initial pH values.

TABLE 6

Average amount of methane consumed by cultures of strain 37:146-1 during different periods of incubation at various temperatures

INCUBATION TEMPERATURE	METHANE CONSUMED AFTER			
	5 days	10 days	15 days	20 days
	ml	*ml*	*ml*	*ml*
5 C	0	0	0	0
15 C	0	0	1	2
22 C	2	6	21	34
27 C	3	10	28	59
32 C	3	19	59	100
37 C	2	9	23	42
40 C	0	0	0	0

Temperature. The occurrence of methane-oxidizing bacteria in sediments on the floor of the ocean where the temperature may be perpetually as low as 3 C suggests that such bacteria are active at low temperatures. Methane oxidation in the laboratory by bacteria from the sea has been demonstrated at 3 to 5 C, although the rate was extremely slow. In one experiment an incubation period of nearly 9 months was required to obtain conclusive results. All cultures examined, including those from the deep sea where low temperatures prevail, were most active at temperatures ranging from 15 to 35 C.

Culture 37:146-1 consumed methane more rapidly at 32 C than at higher or lower temperatures, as shown by the data in table 6. The data are based upon duplicate determination. Since the solubilities of gases vary with the temperature, uninoculated controls were incubated at each temperature to correct for this factor. Münz (1915) observed maximum activity of methane-oxidizing bacteria at 30 to 36 C, the limits being 18 and 40 C.

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SUMMARY AND CONCLUSIONS

Methane-oxidizing bacteria appear to occur quite commonly in the topmost layers of marine sedimentary materials and in soil, being particularly abundant where methane and free oxygen are present. Although methane is attacked less readily and by fewer microbial species than higher hydrocarbons, presumably because the latter have more vulnerable points and are thermodynamically less stable than methane, *Methanomonas methanica* (Söhngen) Orla-Jensen (Breed *et al.* 1948) is not the only species endowed with the ability to oxidize methane.

Pure cultures of methane-oxidizing bacteria, isolated from marine materials, are described that failed to utilize peptone, glucose, sucrose, starch, or glycerol as carbon sources. In purely mineral medium, ethane and propane as well as methane were assimilated by some cultures as the sole source of energy. Carbon dioxide was required for the initiation of growth. Ammonium salts, nitrate, peptone, or glutamic acid served as nitrogen sources. Some strains formed nitrite from the oxidation of ammonia.

The growth of the bacteria was accompanied by the disappearance of methane, the consumption of oxygen, and the formation of carbon dioxide. The medium became turbid and it is calculated from the number of cells present that an equivalent of from 10 to 40 per cent of the carbon from the methane oxidized was converted into bacterial cell substances.

Partial pressures producing the most rapid utilization of methane were oxygen 10 to 40 per cent, methane up to 70 per cent, and carbon dioxide 5 to 20 per cent. An atmosphere consisting by volume of 10 per cent carbon dioxide, 40 per cent oxygen, and 50 per cent methane is recommended for cultivating methane-oxidizing bacteria.

The optimum temperature, pH, redox potential, and osmotic pressure seem to be partly a function of the habitat and history of the organisms. Those studied in this investigation were most active at 32 C, pH 6 to 7, and $E_h > +30$ mv.

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Contribution No. 433

THE ANATOMY AND BIOLOGY OF THE MARINE POLYCHAETE THORACOPHELIA MUCRONATA (TREADWELL) OPHELIIDAE

BY

BAYARD H. McCONNAUGHEY and DENIS L. FOX

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THE ANATOMY AND BIOLOGY OF THE MARINE POLYCHAETE THORACOPHELIA MUCRONATA (TREADWELL) OPHELIIDAE

BY

BAYARD H. McCONNAUGHEY AND DENIS L. FOX

THE COMMON "Bloodworm" *Thoracophelia mucronata* (Treadwell, 1914) lives in vast numbers in the sand of beaches along the California coast, rather high in the area exposed during medium and low tides but covered during high tides. It was briefly described by Treadwell (1914) from specimens collected at La Jolla, California. Subsequently it has been recorded at various places from San Diego north to Oregon, and also from the west coast of Vancouver Island, British Columbia. It has also been noticed south of San Diego along the coast of Lower California between San Diego and Ensenada.

The worms live in well-demarcated strips or mats parallel to the shore line and extending the full length of the beach except where interrupted by shingle, rocky shore, or other unfavorable physical factors. Such a worm-bed measures from ten to thirty feet laterally, depending on the width, slope, and character of the beach itself. Within this strip the worms are found in enormous numbers. E. and C. Berkeley (1932) reported that on the west coast of Vancouver Island whole stretches of the beach are tunneled by countless millions of the worms. Johnson (1942) counted 2,183 under a tenth of a square meter of sand (2,024 per square foot) at La Jolla. The senior writer of the present article obtained counts from 1,900 to more than 4,000 per square foot at La Jolla. A conservative estimate based on all counts gives an average in thriving colonies of from 2,500 to 3,000 worms per square foot. (Pl. 26, *a* and *b*.)

Because of its great abundance, *Thoracophelia* is undoubtedly a factor of some importance in the physical and chemical turnover of organic matter on the local sandy shores. It serves as an important food for certain predators, particularly the long-billed shore birds—the sandpipers, godwits, and curlews, which can be seen in flocks digging the worms during medium and low tides, and leaving areas of the beach pitted and scarred in a characteristic manner.

In the laboratory, *Thoracophelia* has served as an important and economical food for various fishes and other experimental animals, and finally, it has been shown by Fox *et al.* (1948) to possess some unusual and interesting physiological characteristics.

In spite of its great abundance, ready availability, and ecologic interest, little seems to be known about this worm. Treadwell's brief description of the external anatomy and certain biochemical studies by Fox and his associates appear to be the only papers dealing with *Thoracophelia* in any detail. Hartman (1944) gives a few distribution records. Very brief accounts are also found in some general works dealing with seashore life (Johnson and Snook, 1929, Rickets and Calvin, 1939). For this reason it seems desirable to present a more complete account of the anatomy and biology of these worms.

Brown (1938) published a careful anatomical study of a related species, *Ophelia cluthensis*, occupying a similar ecologic niche in the beaches of England. It is of interest to compare *Ophelia* with the local species.

MATERIALS AND METHODS

Anatomical studies were made by dissection of preserved individuals and by study of sections. Some details were best studied by viewing under the microscope young living worms two or three millimeters in length.

The worms were maintained in the laboratory in earthenware flowerpots. The hole in the bottom of the pot was plugged with cotton; the vessel was then nearly filled with damp sand containing many of the living worms, and was set in a shallow pan (*ca.* 1 inch deep) of running sea water. The worms have lived well for several months under these conditions. They are easily injured in digging and handling the sand. To avoid this when changing the sand or removing worms for study, the sand was washed out through the hole in the bottom of the pot with a gentle stream of sea water, the worms being retained on a screen.

By burying the worms in wet sand stained with methylene blue, and alternately in unstained sand, it was possible to study the rate at which the sand in the gut is replaced (see Fox *et al.*, 1948). The worms ingested the stained sand as readily as the unstained. Keeping the worms for a prolonged period in stained sand resulted in staining certain structures in the body with no apparent harm to the worms. The stained sand retained its color well and was not noticeably affected during passage through the gut of the worms.

During the breeding season ripe sperm and eggs were readily obtained by slitting mature worms in the thoracic region. The trochophore larvae lived well in small jars of sea water for about ten days, by which time some of them had reached the metatrochophore stage. We have not succeeded in carrying any of them through to completed transformation.

DESCRIPTION OF THE ADULT WORM

External anatomy.—Preserved adult worms (pl. 27, fig. 1) are commonly 22 to 30 mm. long by about 1 to almost 2 mm. in diameter. In life they have considerable ability to stretch out and contract.

The body consists of the prostomium, 38 setigerous somites and the terminal pygidium. A relatively distinct constriction marks the position of the first internal septum. Aside from this and the last four segments of the trunk in front of the pygidium the somites are not very clearly marked off from each other. Furthermore, each is marked by four secondary annulations almost as clear-cut as those between the somites.

The prostomium is small, conical, drawn out into an acute point anteriorly and without tentacles or palps. The mouth is a transverse ventral slit behind the prostomium, shifted back so that it lies beneath the dorsal portion of the first setigerous somite. Above the mouth on either side is a small nuchal groove just behind and below which arise the first group of small setae, which were overlooked by Treadwell (1914). The setae of the second somite (first of Treadwell) arise at the sides of the thorax just anterior to the groove marking the position of the first septum.

They are somewhat longer and more prominent than any other setae of the body except those arising from the three posterior telescoped segments of the trunk. All the setae are simple and hairlike. In life, an alternating swelling and deflation of the head region in front of the first septum (the head plus the first two setigers), correlated with movements of the body, plays an important role in the burrowing.

When everted, the pharynx (pl. 27, fig. 2) consists of 3 soft, ciliated, unarmed lobes extending only slightly beyond the head.

The eyes (pl. 27, fig. 4) are not evident except when the worm is magnified and viewed by transmitted light. They are beneath the body wall, lying as three dark spots on the surface of the brain just behind the prostomium. One eyespot occurs on either side of the forepart of the brain, the third being asymmetrically placed on the left hind part of the brain. Occasionally the posterior eye is missing.

The thoracic region is somewhat swollen, rounded dorsally and flattened ventrally, and consists of 13 somites. The last three of these are transitional, showing the beginnings of the lateral and ventral grooves characteristic of the abdominal region. On the tenth segment there is a large, vertical, glandular ridge on either side of the body, causing the body wall to project a little in flange-like fashion. Each somite bears on either side two small, inconspicuous groups of short setae.

The abdomen comprises about two-thirds of the body length. It consists of 18 segments bearing paired branchiae on either side followed by 4 elongated, swollen, poorly defined segements without branchiae, 3 short, partly telescoped segments bearing long setae, and the terminal pygidium. There is a deep ventral groove and shallow lateral grooves throughout the gill-bearing region. Dorsally the boundary of each abdominal somite is marked by a conspicuous dorsal pore. The last five to seven thoracic segments also have these pores, but anteriorly they become smaller and inconspicuous.

The pygidium (pl. 27, figs. 1 and 3) bears a large ventral cirrus. The lateral walls of the pygidium are produced into six or seven smaller cirri on each side, forming a fringe around the anus. In the dorsal wall of the rectum, in the three telescoped segments anterior to the pygidium, are two large, thick-walled, bent outfoldings from the gut, bearing longitudinal strips of especially strong, densely crowded cilia on their dorsal walls (pl. 27, fig. 3, and pl. 30, fig. 22). These beat intermittently in unison, creating a current in an anterior direction from the anus. They probably serve a respiratory function.

Internal anatomy.—The internal anatomy is characterized by the almost complete lack of septa, allowing the coelomic fluid to flow freely back and forth with each movement of the body. The only septa present are between the second and third, and the third and fourth, setigerous somites of the thorax. They are reflected back over the esophagus, forming a large, blind sac, the injector organ, opening anteriorly into the coelomic cavity of the head region (pl. 27, fig. 5). The first septum is much more muscular than the second. The two are distinct just anterior to the injector organ, but the organ itself appears to be composed of only one wall derived chiefly from the anterior septum, rather than of two distinctly separate sacs as described for *Ophelia cluthensis.*

Through its own muscular action and because of variations in the pressure of the coelomic fluid with different muscular movements of the worm, this sac alternately withdraws the coelomic fluid from the head region, deflating it, or forces it into the head region, causing it to swell into a bulbous shape. This alternate swelling and deflation of the "head" is important in the burrowing of the worm. The coelomic fluid anterior to the septa is clearer than that in the rest of the body. It does not contain the peculiar coelomic corpuscles of the latter, and in the breeding season does not contain eggs or sperm, which fill the coelom in the rest of the body.

The vascular system is closed. The blood is bright red in contrast to the coelomic fluid, which is of a light straw color. The red component was identified as hemoglobin by spectroscopic and chemical tests (Fox *et al.*, 1948).

In the abdominal region the dorsal blood vessel is replaced by a large blood sinus in the walls of the intestine, as is characteristic of the worms in this and closely related families (pl. 29, fig. 21). This sinus gives off in each somite a vessel passing to the gills and thence to the ventral blood vessels. The ventral vessel also gives off a smaller branch, which returns blood to the dorsal sinus in each somite. At the junction of the mid-gut and intestine (pl. 27, fig. 5) the dorsal sinus gives rise to the definitive dorsal blood vessel which passes forward through the thoracic region to the brain, giving off lateral segmental branches in each somite of the anterior part of the thoracic region. Upon reaching the brain the dorsal vessel divides into two branches, passing posteriorly and ventrally roughly parallel to the circumpharyngeal nerve connectives (pl. 27, fig. 4). These join ventrally to form the ventral blood vessel passing back beneath the esophagus. Just lateral to the juncture of the circumpharyngeal nerve connectives and of the two blood vessels, in front of the septum, are two glands the function of which is as yet unknown, which stain conspicuously with methylene blue in worms fed stained sand.

The first branches of the dorsal vessel behind the head pass to the posterior side of the first septum on either side, forming here an intricate plexus of small vessels from which a ventral vessel arises on each side passing into the ventral blood vessels. The next three sets of branches of the dorsal vessel behind this pass to the body wall at the base of the rudimentary parapodia of each segment, respectively; here they give rise to a small cluster of short, blind, digitate vessels the ends of which are free in the coelom. These blind vessels are contractile and alternately fill and empty themselves of blood. From the base of each such cluster a ventral branch returns the blood to the ventral blood vessel.

At the junction of the esophagus and stomach the ventral blood vessel disappears from view, passing inside with an infolding of the ventral wall of the gut to form the large stomachal sinus carrying blood posteriorly in the folds of the ventral typhlosole and around the outer walls of the stomach (pl. 27, fig. 5, and pl. 29, fig. 20). At the junction of the stomach and intestine the ventral vessel reappears and continues posteriorly as already described. At the point of its reappearance it receives from each side a branch from the dorsal blood vessel arising just anterior to the "heart."

The excretory system (pl. 30, fig. 23) differs widely from that described for *Ophelia cluthensis* by Brown (1938). In the latter species, according to Brown, the nephridia are limited to segments 13, 14, and 15 and each consists of a ciliated nephridial canal with an open nephrostome opposite the gill in front.

In *Thoracophelia mucronata* the nephridia are not as limited in their distribution, and are of the protonephridial type, with rosettes of solenocytes projecting into the coelom from the lobulated sides of the blind ends of the nephridial tubes. These nephridia lie along the segmental efferent branchial blood vessels between the base of the gills and the intestine. From the base of each gill a long, ciliated, nephridial canal, not lined with solenocytes, extends posteriorly nearly to the next gill. Nephridia have been found in all somites from the fifth branchial back to and including the first postbranchial. In very small worms distended by immersion in fresh water and slightly flattened beneath a cover slip, they can be studied in life under the microscope. Some of the posterior nephridia were at times seen to be branched so as to lie along both the branchial vessels.

The digestive tract is divided into three major portions: the fore-gut, stomach, and intestine.

The fore-gut consists of the mouth, pharynx, and esophagus. The mouth is a transverse, somewhat wrinkled, slit in the ventral side of the head region. When everted, the pharynx consists of three soft ciliated lobes with which the worm gathers in sand. In its normal position, withdrawn, it consists of an enlarged part of the alimentary tract with the walls thrown into multiple, deep longitudinal folds nearly filling the lumen (pl. 28, fig. 18). The esophagus (pl. 28, fig. 19) is a straight tubular part, narrower than either the pharynx or stomach.

The stomach (pl. 27, figs. 5, 6, 7, and pl. 29, fig. 20) is larger in circumference than either the esophagus or the intestine. Ventrally it is infolded to form a large typhlosole, which longitudinally is multiply grooved and which occupies the greater part of the lumen and carries sinuses representing the ventral blood vessel (pl. 29, fig. 20).

The cells of the wall of the stomach, and to a lesser degree of the intestine, are heavily loaded with dark greenish granules, which give the stomach a dark appearance that shows through the body wall. Parts of this wall may peel off in sheets during dissection, looking superficially like bits of plant detritus (pl. 27, figs. 8 and 9). On either side of the stomach, a short distance posterior to its junction with the esophagus, is a small gland the ducts of which meet and enter in the mid-ventral line at the junction of the stomach and esophagus (pl. 27, figs. 5 and 6).

The intestine is a relatively simple, thin-walled tube with a large dorsal blood sinus almost surrounding the lumen (pl. 29, fig. 21). Posteriorly, in the swollen region of the body just anterior to the pygidium, its ventral wall is infolded, forming a high internal ridge which continues beyond the anus as the large ventral anal cirrus of the pygidium. Dorsally in the last three segments the wall of the rectum is folded out, forming the two peculiar, strongly ciliated organs already mentioned (pl. 27, fig. 3, and pl. 30, fig. 22).

The sexes are separate. The sperm and the eggs are liberated into the coelomic fluid very early in their development, the eggs singly, the sperm in packets of a few hundred each. Here they develop until ready for fertilization.

ECOLOGY

The worms are always found massed together, all the worms of a colony being at about the same depth in the sand at any given place. The limits of the colony are usually very definite, especially along the seaward side. Here it is often possible to draw a line in the sand, on one side of which there are no worms, while on the other side each shovelful of sand may contain hundreds.

When the tide falls, the worms come up near the surface and are found within the top two or three inches of sand. With the return of the tide, they burrow as much as a foot or more below the sand surface. When, on unusually long exposure, the sand of the upper part of the colony beings to dry out, the worms retreat more deeply into the damp sand below. In general the colony is limited on the upper margin by the part of the beach which dries out to a depth of a few inches between tides, on the lower margin by the zone in which the sand remains saturated. At low tide the animals can be induced to burrow more deeply by pouring sea water on the sand and thus simulating the returning tide.

As the tide falls and the worms come to the surface while the sand is still soft and saturated, their presence can be detected by a slight movement of the sand as they move about just beneath the surface, and by small depressions produced when the wet sand falls into their burrows.

As the sand becomes less saturated and firmer, the movement of a worm just beneath the surface often causes a few grains of sand to fall into the burrow, forming a minute hole in the sand. More sand may cave in or adhere to the worm as it passes just beneath the surface, exposing a slightly greater area of the burrow. Thus the area occupied by the worm bed may quickly become pitted with thousands of tiny, characteristic holes (pl. 26, *a* and *b*). Sometimes by holding one's ear close to the sand one can hear a faint snapping or popping sound throughout the area, probably caused by the collapse of countless minute bubbles of air.

So far as the writers have observed, the worms never actually crawl out upon the surface of the sand. They are seen there only briefly when washed out by a wave, and immediately burrow back again. The formation of the little pits in the sand has been observed both on the beach and in the laboratory, and the worms were never seen to crawl out upon the surface or to expose their bodies at all.

In the laboratory, as in nature, the worms exhibit a definite negative phototropism. If placed in a pan to which light is admitted only at one end, they tend to gather in the dark end of the pan.

FOOD

The fact that so great a number of worms live and maintain themselves in apparently clean beach sand lends considerable interest to the question of their food supply. The worms move slowly, have a short, unarmed pharynx, and are not equipped to capture active prey, as are many polychaetes. Nor are they provided with a mechanism for concentrating plankton from the water, as are many sedentary shore organisms. At the outset of this research it was thought likely that the food consisted chiefly of plant detritus from seaweeds, filamentous algae, and the like, thrown up on the beaches, and perhaps of diatoms and other microscopic plankton. But as no increase in the concentration of worms was observed around partly buried, decaying algae on the beach, and since repeated examinations of the gut contents of worms freshly taken from the beach showed only sand grains without any plant tissues or fragments of small animals or appreciable numbers of phytoplankton, we have developed a different concept.

It appears that the worm derives its nutrition largely from the organic matter adsorbed to the sand grains, together with whatever protozoa, bacteria, and other small organisms it may ingest, adhering to the sand or otherwise associated with it. Many of the sand grains were observed to have a few very small sessile diatoms attached to their surface, but these are not believed to be of much importance to the worms since they seem to pass through the gut unchanged and still attached to the sand grains. Counts made of small diatoms attached to the sand grains from the area of the worm colony, from sand in the worm's gut, and from sand in the worm's feces, showed that there was no significant difference. The microscopic appearance of these sessile diatoms was also unaltered.

TABLE 1

MAGNITUDE OF FEEDING OPERATIONS OF THORACOPHELIA MUCRONATA ON CALIFORNIA SEA BEACHES NEAR LA JOLLA

Volume of damp sand in the bed	52,800 cubic feet
Weight of sand in the bed (*ca.* 131 lbs./cu. ft.)	3,460 tons
Weight of actual sand (subtracting *ca.* 18 per cent for the water)	2,820 tons
Total number of worms present (estimate)	158,000,000
Total weight of worms present (estimate) (*ca.* 0.04 gr. each)	7 tons
Weight of sand cycled annually (*ca.* 84 gr. per worm)	14,600 tons
Organic matter in sand cycled annually by the worms (*ca.* 1 per cent	146 tons
Relative efficiency of worms in maintaining a standing population, if an annual cycle is assumed	0.96 per cent
Ratio of sand cycled annually to the sand in the worm bed. (Equivalent to cycling all the sand in the bed about once every 10 weeks)	5.2 to 1

To determine whether the amount of organic matter available on the sand to the feeding worms might be sufficient for their nutrition, a study was made of the amount of organic matter in the sand derived from the area occupied by the worms, of the amount of worm tissue present, and of the rate of cycling of the sand by the worms, to try to arrive at some idea of their food budget.

In order that the results may be made to present a more clear-cut picture of the order of magnitude of the operations of these worms in our local beaches, the results from our samples were recalculated to apply to a theoretical worm bed one mile in length, ten feet in width, and one foot in thickness. The populations are based upon counts of samples. The values for the density of sand, the rate of its ingestion, and so on, are based upon the measurements of samples and the results of experimental feeding of the worms alternately with stained and unstained sand; this indicated that they replace the sand in the gut about every fifteen minutes. The figures here given (table 1) are taken from a table in an earlier paper of ours dealing primarily with the carotenoid metabolism of the worms (Fox *et al.*, 1948).

If we consider the beach as a whole, assuming a wedge 1 mile long, 200 ft. wide and 2.5 ft. thick, which would contain about 7.05×10^4 tons of sand, it appears that the worms in the limited strip defined would cycle about 21 per cent of the beach sand annually.

REPRODUCTION AND DEVELOPMENT

The breeding season extends from about the middle of April into September. Most of the larger worms taken in that interval were found to contain sperm or eggs. The sexes occur in approximately equal numbers. The sperm and the eggs are free in the coelomic fluid from very early stages. When ripe, the germ cells are so abundant as almost to fill the coelom, especially in the thoracic region.

The eggs are disk-shaped, flattened or even slightly biconcave in edge view when taken from the body (pl. 28, figs. 11 and 12). They have a large, clear, germinal vesicle surrounded by densely granular cytoplasm. They are about 65 microns in diameter in the broad view by about 35 microns in edge view. After fertilization, just prior to the formation of the first polar body, the eggs become spherical or broadly oval.

If the body wall of mature worms is broken open in the thoracic region and the eggs or sperm allowed to escape, they can be obtained in any desired numbers. If they are mixed together in a vessel of sea water, fertilization occurs readily. The fertilized egg forms a fertilization membrane, beneath which the polar bodies are given off at one pole. On the side opposite that from which the polar bodies are given off, the membrane is thrown into characteristic wrinkles (pl. 28, figs. 13 and 14). Development is rapid, and within five or six hours after fertilization young trochophore larvae are swimming about in the vessel.

The young trochophores are nearly spherical, but within two or three days an elongation and narrowing of the hyposphere is noticeable and the internal organs are more clearly demarcated. In the episphere are two pigmentary eyespots and three large, unicellular, mucous glands. The latter, in fixed preparations, become stained more deeply than the other cells; they are curved, and project from the body surface like small periscopes. One is in front above the mouth, and one on either side about a fourth of the way round the body (pl. 28, figs. 15 and 16).

The trochophores show a strong positive phototropism, always gathering in a cloud on the illuminated side of their container. They lived well in the laboratory for the first week, but after nine or ten days most of them died. A few were carried through the early stages of transformation, with the formation of setae on two or three somites, and some differentiation of the pygidium, the ventral anal cirrus being distinguishable, as was shown in the eleven-day larva (pl. 28, fig. 17). At this stage the young larva had settled to the bottom and, while still capable of swimming, did not do so unless disturbed, but crawled about on the bottom of the vessel by muscular movements in a wormlike manner.

SUMMARY

Thoracophelia mucronata is an extremely abundant marine polychaete annelid living in large colonies in the intertidal zone of the sandy beaches along the western coast of North America. Adults are negatively phototropic, and remain buried in the sand. Calculations indicate that along a mile of beach there may sometimes be as many as 158,000,000 individuals, representing about 7 tons of worms.

The worms are red to purplish in color, two to four centimeters long, with weakly marked segmentation. The parapodia are greatly reduced and the setae simple, short, and inconspicuous except for long ones borne on the posterior three somites. The prostomium is small, acutely pointed, and without tentacles or palps. The eyes are beneath the body wall on the surface of the brain, three in number, asymmetrically placed, two in front and one behind on the left side. The trunk is divided into a swollen thoracic region which has no gills, and next the abdomen, which bears 18 pairs of branchiae. Posterior to the branchial region are 4 poorly defined, postbranchial somites, and 3 short, telescoped segments bearing long setae. The dorsal wall of the rectum in these last three segments contains two strongly ciliated outpocketings which create an inward current from the anus and may serve a respiratory function. The pygidium bears a single large ventral cirrus and a fringe of 6 or 7 smaller lateral cirri on each side.

The internal anatomy is characterized by the lack of septa except two in the anterior part of the thorax, and by the replacement of the dorsal blood vessel with a large blood sinus in the wall of the intestine in the abdominal region. The two septa are reflected back over the esophagus as a large blind sac which alternately inflates and deflates the head region by forcing in and withdrawing coelomic fluid. This swelling and collapsing of the head region by the injector organ is important in the burrowing of the worm.

The excretory system is of the protonephridial type and the nephridia are distributed from about the fifth branchial somite to the first postbranchial somite inclusively.

The sexes are separate, occurring in about equal numbers. In southern California the breeding season lasts throughout the spring and summer. The trochophore larvae exhibit positive phototropism and are free-swimming for about ten days.

The worms seem to ingest only sand and to depend largely for their nutrition upon the organic matter adsorbed to the sand grains. They replace the sand in the gut about every fifteen minutes, and in a year's time each 40-milligram worm may cycle at least 84 grams of sand. A colony of worms in a strip of beach sand 1 mile long, 10 feet wide, and 1 foot thick, containing an average of 3,000 worms per square foot, would cycle approximately 14,600 tons of sand annually, or almost 21 per cent of all the sand on the La Jolla beach. This would give them about 146 tons of organic matter, and a relative efficiency of about 0.96 per cent in maintaining a standing population, assuming an annual life cycle.

The authors wish to express grateful acknowledgment to the following: the Rockefeller Foundation for a grant-in-aid; Mr. Sheldon C. Crane and Mr. Arthur S. Lockley for their generous assistance in technical details and for excellent photographs by the latter; and to Professor Wesley R. Coe for his unfailing friendly interest. Dr. Olga Hartman of the Hancock Foundation, University of Southern California, has given us valuable suggestions and references.

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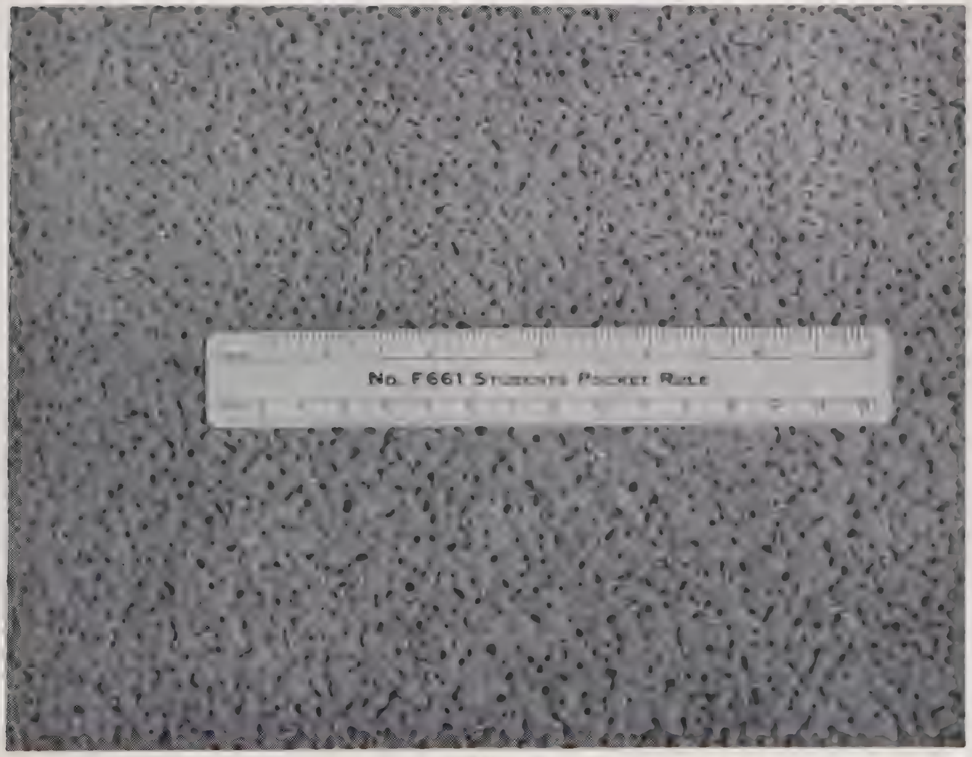
PLATES

PLATE 26

a. Small part of beach just north of the Scripps Institution pier, showing area, occupied by part of a worm colony, darkened by the presence of thousands of small holes made in the sand by the worms. Limits of the colony are emphasized by a dotted line. Photograph by Arthur S. Lockley.

b. Close-up view of part of the area in *a,* above, showing the sand honeycombed by worm burrows. Photograph by Arthur S. Lockley.

a


No. F661 Students Pocket Rule

b

PLATE 27

Fig. 1. Adult worm from the right side. Somites are numbered beginning with the first setigerous somite of the head.

Fig. 2. Anterior end of preserved worm with the pharynx everted.

Fig. 3. Pygidium in dorsal view, showing the position of the two strongly ciliated rectal organs shown in cross section in figure 22. From small living worm.

Fig. 4. Anterior part of head as seen by transmitted light, showing the brain with three eyespots, and the dorsal blood vessel with its branches parallel to the circumpharyngeal nerve connectives.

Fig. 5. Anterior part of the digestive tract exposed by removal of the body wall. The injector organ by which coelomic fluid is forced into the head and withdrawn from it is much contracted. In living worms it may reach back the full length of the esophagus. (The anterior part of the ventral blood vessel and the lateral branches of the dorsal blood vessel in the thoracic region are not shown.)

Fig. 6. Junction of esophagus and stomach in ventral view.

Fig. 7. Stomach and intestine, shown with the outer wall removed, exposing the lumen and the large ventral typhosole of the stomach.

Fig. 8. Group of cells from the area near the junction of the esophagus and stomach, showing light concentration of greenish granules.

Fig. 9. Isolated cells from the wall of the stomach, with heavy concentration of granules.

Fig. 10. Sperm cell.

Fig. 11. Mature egg cell just taken from the coelom.

Fig. 12. Same egg cell in edge view.

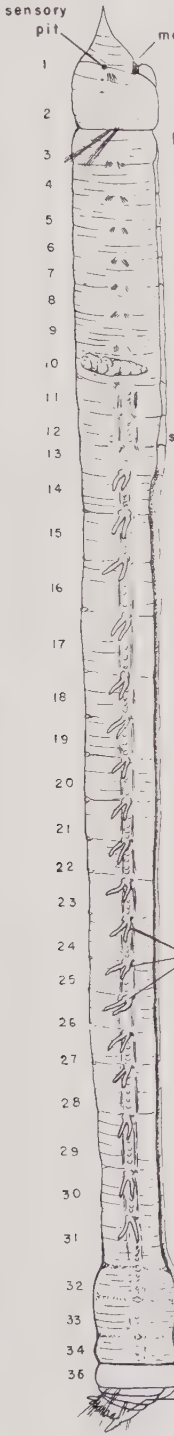
Fig. 13. Fertilized egg after the elimination of the polar bodies.

Fig. 14. First cleavage, showing the two unequal blastomeres.

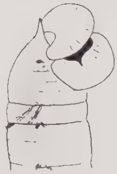
Fig. 15. Trochophore larva, about twenty-four hours old.

Fig. 16. Trochophore larva, four days old.

Fig. 17. Metatrochophore, eleven days old.


sensory pit
mouth
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
36
branchiae (gills)
pygidium

1



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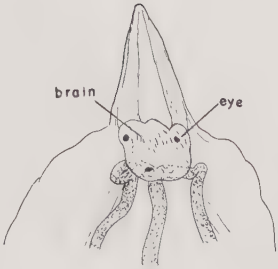

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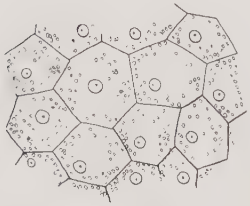

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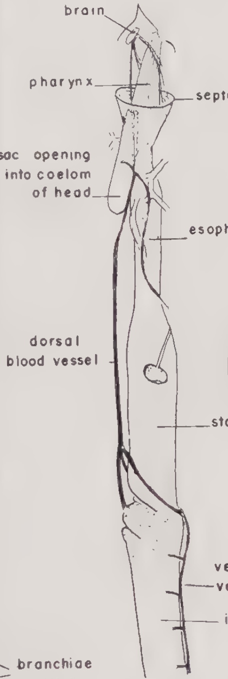
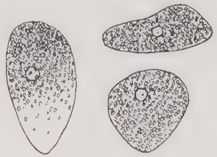

brain
pharynx
septum
sac opening into coelom of head
esophagus
dorsal blood vessel
stomach
ventral blood vessel
intestine

5



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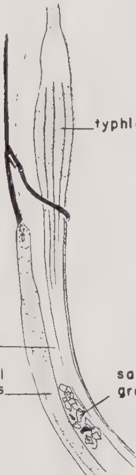
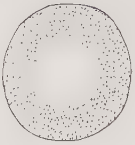

typhlosole
lumen
dorsal sinus
sand grains

7

10



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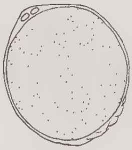

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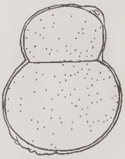

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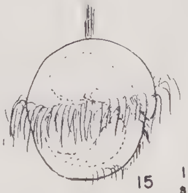

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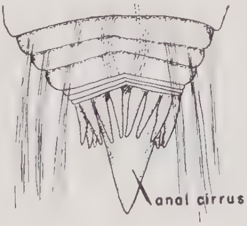
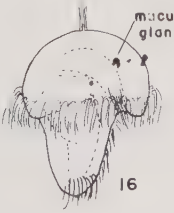
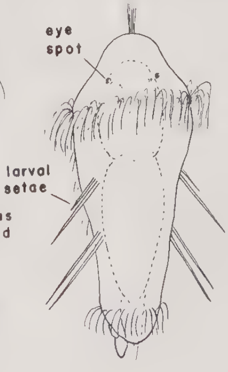

anal cirrus

3


mucus gland

16

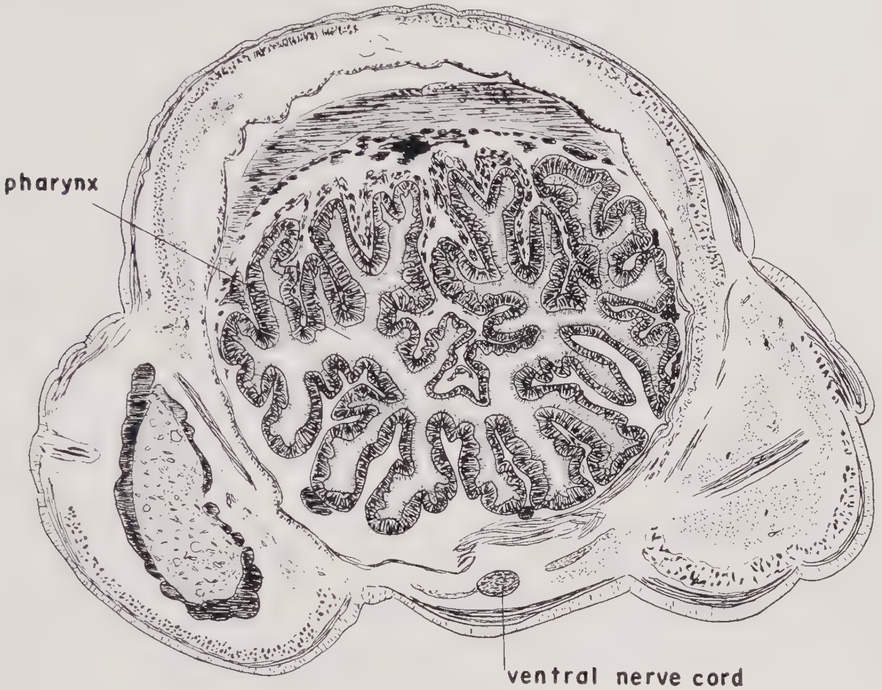

eye spot
larval setae

17

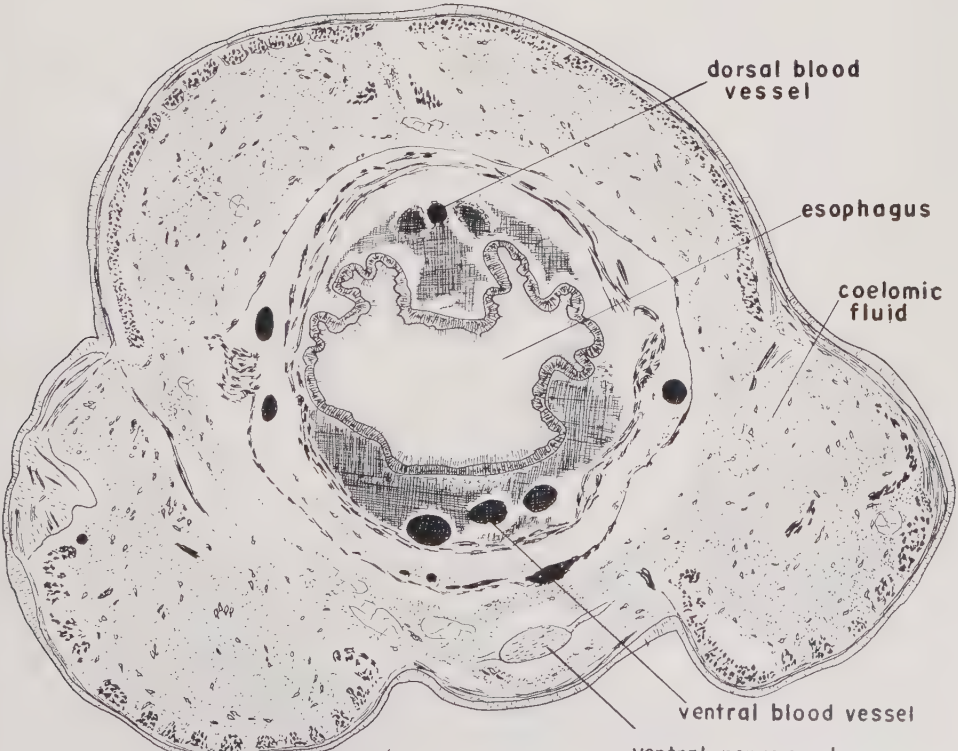
PLATE 28

Fig. 18. Transverse section of the pharyngeal region.

Fig. 19. Transverse section through the esophagus.


pharynx
ventral nerve cord

18

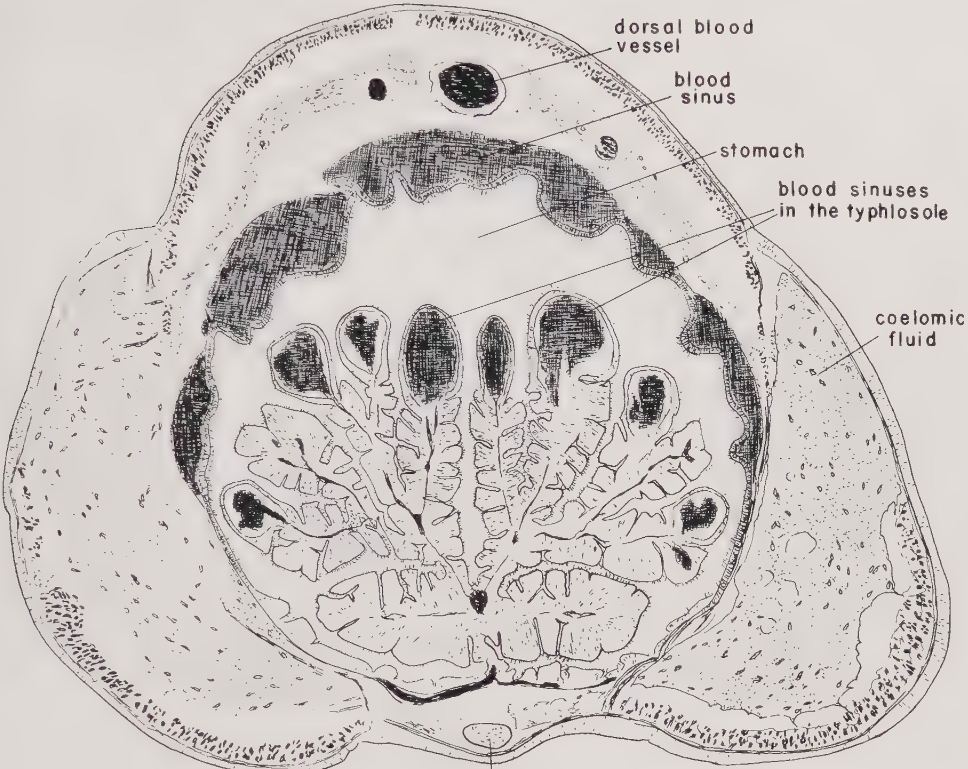

dorsal blood vessel
esophagus
coelomic fluid
ventral blood vessel
ventral nerve cord

19

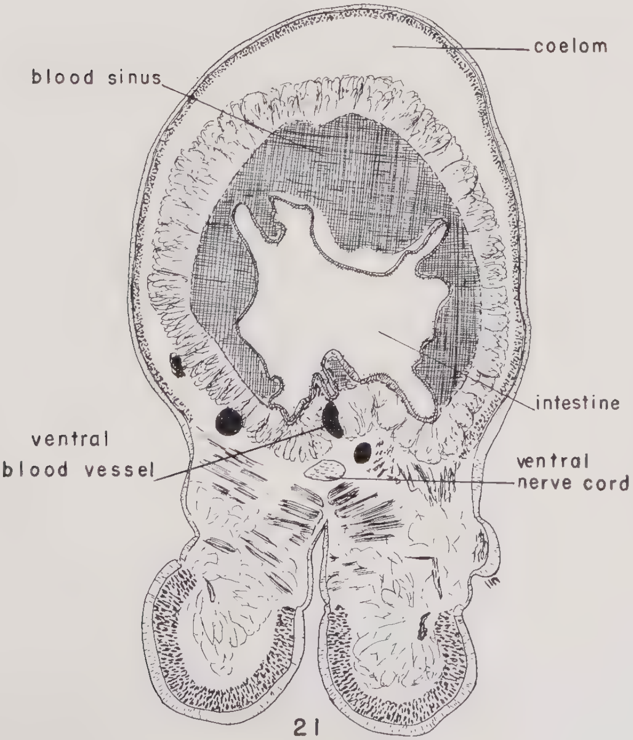
PLATE 29

Fig. 20. Transverse section through the stomach.

Fig. 21. Transverse section through the intestine.


dorsal blood vessel
blood sinus
stomach
blood sinuses in the typhlosole
coelomic fluid
ventral nerve cord

20


coelom
blood sinus
intestine
ventral blood vessel
ventral nerve cord

21

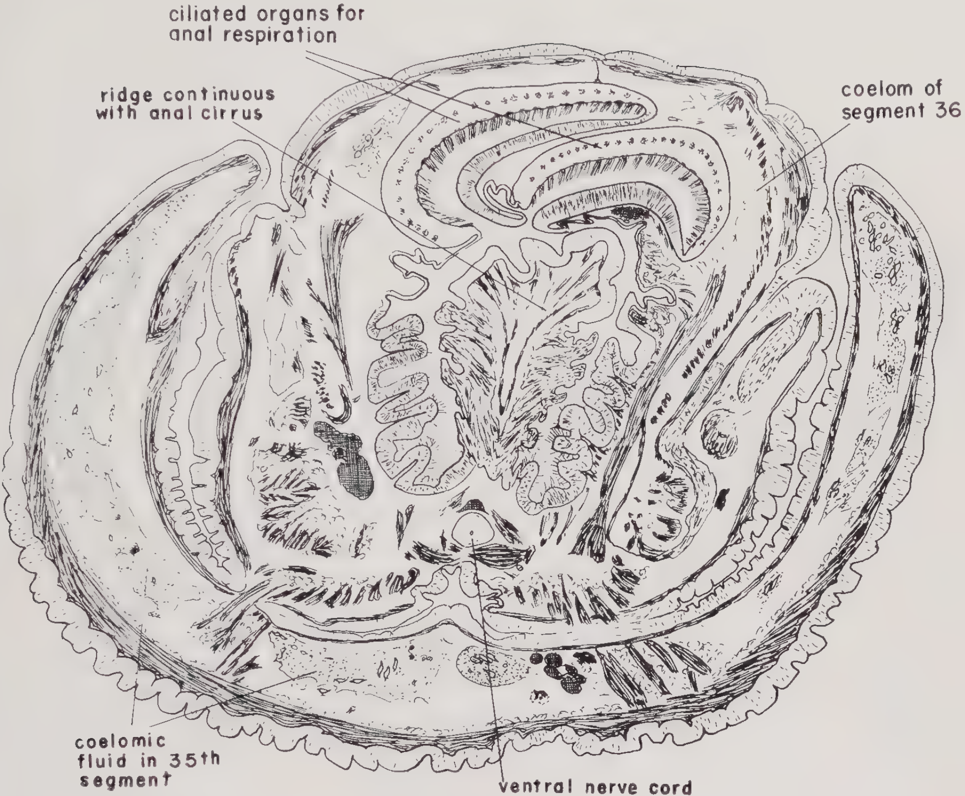
PLATE 30

Fig. 22. Transverse section through the pygidium.

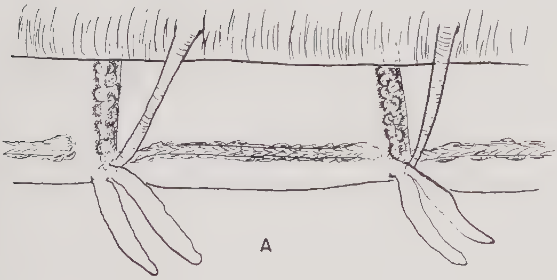
Fig. 23, *a*. Semidiagrammatic view of the side of an abdominal branchial somite of a small living worm, showing the relationships of the nephridia to the blood vessels, intestine, and gills.

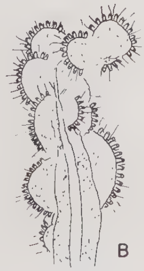
Fig. 23, *b*. Terminal part of one nephridium enlarged to show rosette-like clusters of solenocytes.

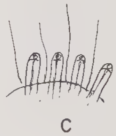
Fig. 23, *c*. Further enlargement of a few solenocytes to show the inner flagella and the outer flagella arising between the solenocytes.


ciliated organs for anal respiration
ridge continuous with anal cirrus
coelom of segment 36
coelomic fluid in 35th segment
ventral nerve cord

22


A


B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23

Contribution No. 434

Transaction, American Geophysical Union Volume 30, Number 6 December 1949

SURF BEATS

W. H. Munk

(Contribution from the Scripps Institution of Oceanography, New Series, No. 434)

Abstract--Irregular oscillations of the near-shore water level, with periods of the order of several minutes, are correlated with fluctuations in the height and period of incoming waves.

An instrument for recording long-period ocean waves [MUNK, IGLESIAS, and FOLSOM, 1948] has been in operation since January 1948 at the end of the Scripps Institution pier, La Jolla, California. The instrument, which is sensitive to waves whose frequencies fall between those of the wind-generated waves and those of the astronomic tides, is called the tsunami recorder, as it is especially adapted to the period range of tsunamis. In the presence of high wind waves the tsunami recorder reveals irregular oscillations of several minutes' period. These oscillations have a broad frequency spectrum, which reaches a maximum in amplitude for periods of the order of two minutes, and drops off for longer and shorter periods by about six decibels per octave.

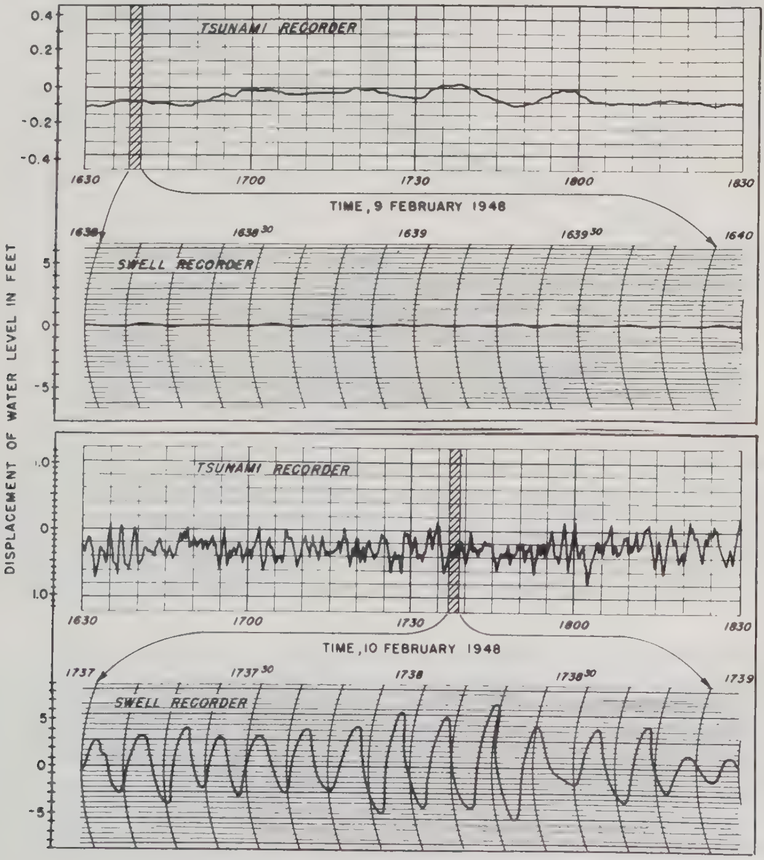

Fig. 1--Comparative records from tsunami recorder and swell recorder on two successive days

Figure 1 shows comparative records taken on two successive days by the tsunami recorder and by a swell recorder [FOLSOM, 1949]. The time scales bear a ratio of 60:1, and the shaded band on the tsunami record shows the duration of the swell record. The height scales on the tsunami and swell records refer to periods of two minutes and eight seconds, respectively. The swell recorder is about equally responsive to waves of eight-second and two-minute periods, whereas the tsunami recorder is forty times as responsive to the two-minute waves as to the eight-second waves. The swell recorder is located 1000 ft off the end of Scripps Pier in water of about 40-ft depth, (see Fig. 2); it records pressure fluctuations at the sea bottom against time, and these can be interpreted in terms of the oscillations of the sea surface. Both instruments are connected by electric cables to a building ashore where the waves are recorded. On the afternoon of February 9 the sea was glassy calm (wave heights less than three inches), and the tsunami record smooth, except for two-inch undulations of approximately 20-min period, which are typical of certain meteorological conditions off the coast of California. Twenty-four hours later the swell recorder showed waves of seven- to nine-second period up to ten feet in height, and the tsunami recorder revealed irregular two- to three-minute oscillations up to 0.8 feet in height.

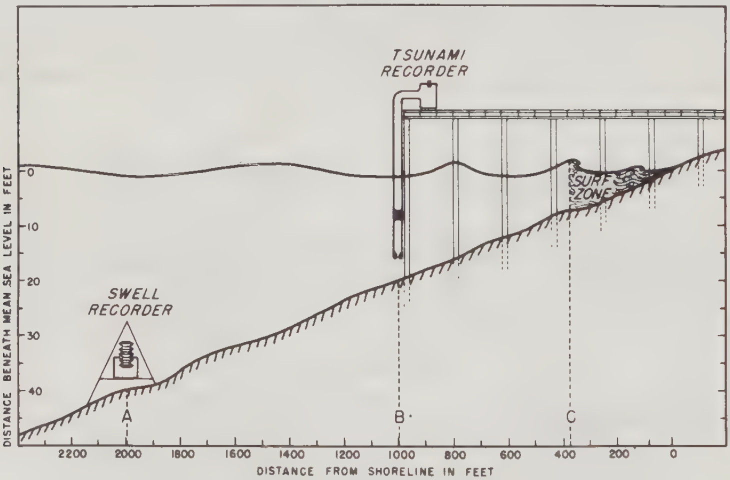

Fig. 2--Location of swell and tsunami recorders relative to the Scripps Institution pier at La Jolla

Figure 3 shows the height of the significant waves (average of the highest one-third) on the tsunami and swell recorders for two storms. Although the determination of the numerical values of significant wave height from wave records is subject to some personal judgment, the figure indicates a definite relationship between wave heights recorded by the two instruments. From 103 measurements conducted during February and March, 1948, (see Table 1) it appears that at the Scripps Institution pier on the average the height of wind-generated waves equals 11 times the height of the waves on the tsunami recorder.

The two- to three-minute oscillations are related to the variability in the height and period of the incoming waves. To anyone wading in shallow water it is apparent that a rapid succession of high breakers temporarily raises the water level. John Isaacs (personal communication) has observed such changes in sea level up to 16 ft at Twin Rocks Beach, Oregon. To investigate this quantitatively, we note that according to the solitary wave theory [MUNK, 1949] the volume of water transported into the surf zone by each breaking wave is proportional to the square of the breaker height. On a 20-min section of swell record (see Fig. 4) starting at $t = 0$ ($11^h 02^m 20^s$) and ending at $t = 1080$ sec ($11^h 20^m 20^s$) the wave crests are numbered 1, 2, . . .n, . . .N. Let n designate the nth wave arriving at a time t_n and having a height H_n. The shoreward transport during the interval O to t_n is proportional to $\sum_n H_n^2$, the summation being carried out with respect to wave crests. For the entire 20-min interval, the shoreward transport $\sum_N H_n^2$ must equal approximately the seaward transport due to a superimposed return flow, rip currents, and other processes [MUNK, 1949]. Assume the seaward transport to be constant with time. Then

$$\sum_n H_n^2 - (n/N)\sum_N H_n^2$$

Table 1--Comparative heights of waves on tsunami recorder (period two to three minutes) and swell recorders (period seven to nine seconds)

Range in wave height	Number of measurements	Significant wave height		Ratio $\frac{\text{Col 4}}{\text{Col 3}}$
		Tsunami recorder	Swell recorder	
1	2	3	4	5
ft		ft	ft	
<1	15	.085	0.8	9.5
1 - 2	36	.15	1.6	10.7
2 - 3	24	.20	2.6	13.0
>3	28	.35	4.6	13.1
Weighted mean				11.4

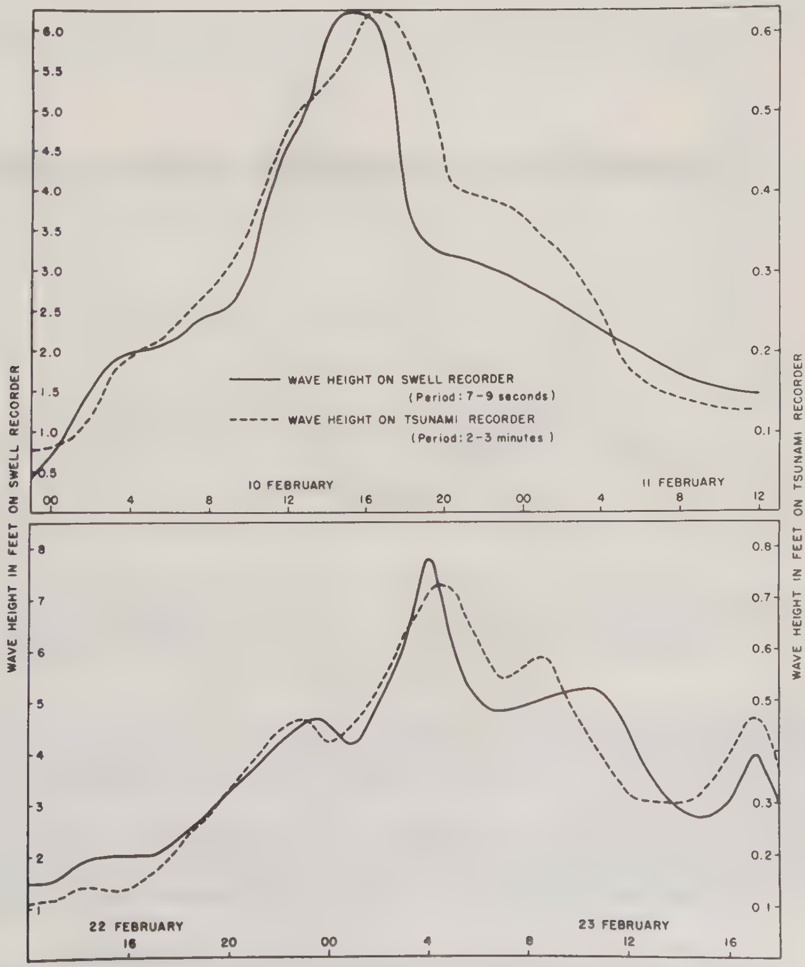

Fig. 3--Comparative heights of waves shown by the tsunami and swell recorders for two storms; the height scale on the tsunami record is exaggerated ten times relative to the height scale on the swell records represents the excess (in arbitrary units) of the shoreward transport over the seaward return between the times 0 and t_n. This quantity is marked "integrated swell record" in Figure 4.

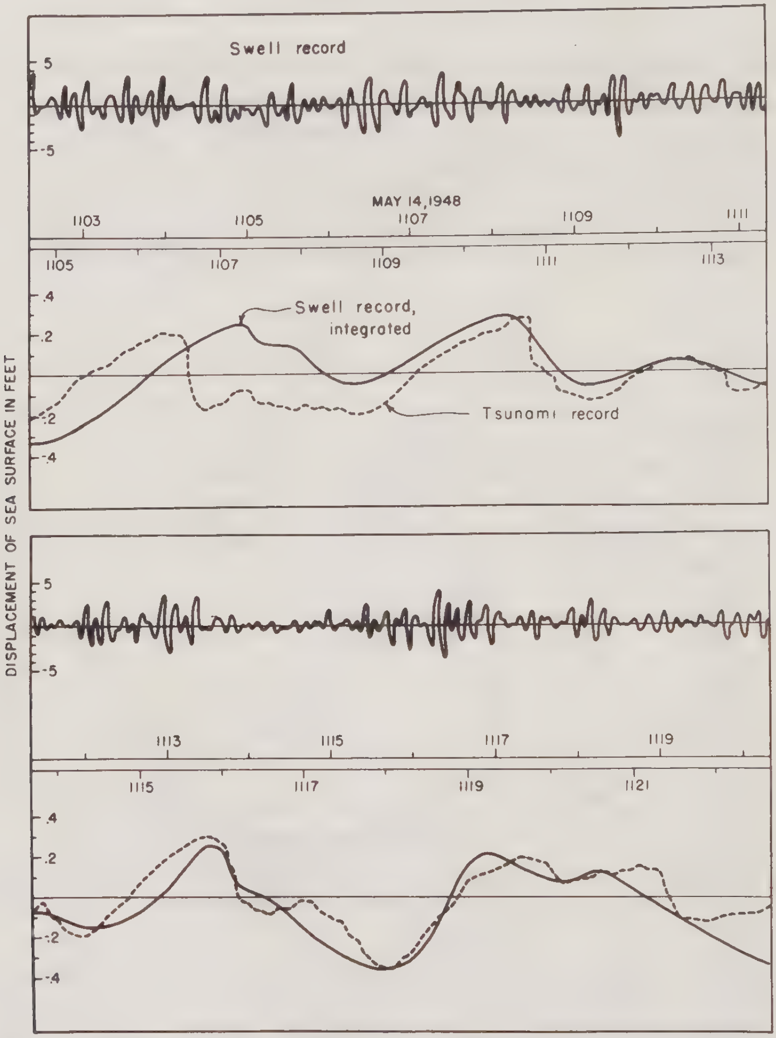

Fig. 4--Detailed comparison of waves on swell and tsunami recorders; the upper time scale refers to swell record and integrated swell record; the lower time scale refers to tsunami record, and is displaced 140 sec relative to upper time scale

During the 20-min interval shown in Figure 4 the tsunami recorder was run at 60 times its normal speed in order for the time scales on the two records to be identical. The integrated swell record resembles the tsunami record, provided the two records are displaced by 140 sec.

This lag Δt of the tsunami record relative to the integrated swell record results from the tim involved for the waves to travel from the swell recorder past the tsunami recorder to the surf zone for the two- to three-minute oscillations to travel from the surf zone back to the tsunami recorder (Fig. 2), and the phase lag of the tsunami recorder, about 90° for waves of two-min periods. Thus

$$\Delta t = \int_A^B (1/V)dx + \int_B^C (1/V)dx + \int_C^B (1/V)dx + (90^\circ/360^\circ)120$$
$$= 42 + 34 + 30 + 30 = 136 \text{ seconds}$$

Table 2--Computed horizontal orbital velocities, displacements, and pressure fluctuations at ocean bottom associated with waves of eight-second period and 4.5-ft height in deep water, and with surf beats of two-minute period caused by these waves

Depth	Height		Horizontal orbital velocity		Horizontal displacement		Pressure	
	Waves	Surf beat	Waves	Surf beat	Waves	Surf beat	Waves	Surf beat
ft	ft	ft	ft/sec	ft/sec	ft	ft	ft/sea water	ft/sea water
7.5[a]	6.0	0.6	5.9	0.62	15	24	5.6	0.60
10	5.2	0.5	4.4	0.45	11	17	4.7	0.50
20	4.5	0.47	2.5	0.30	6.4	11	3.7	0.47
50	4.2	0.39	1.1	0.16	2.8	6.1	2.4	0.39
100	4.3	0.31	4.7×10^{-1}	0.088	1.2	3.4	1.2	0.31
200	4.5	0.26	8.0×10^{-2}	0.052	2.0×10^{-1}	2.0	1.9×10^{-1}	0.26
500	4.5	0.21	1.2×10^{-4}	0.027	3.1×10^{-4}	1.0	3.0×10^{-4}	0.21
1000	4.5	0.18	8.1×10^{-9}	0.016	2.0×10^{-8}	0.6	2.1×10^{-8}	0.18

[a] Breaking point

compared to a measured time lag of 140 sec. The values have been obtained by numerical integration, setting eight seconds and two minutes for the periods of incoming and outgoing waves, respectively, and substituting

$$V = \sqrt{(g \tanh kh)/k}\,(1 + 2kh/\sinh 2kh)/2$$

for the group velocity of waves of length $2\pi/k$ at depth h. The distances are those shown in Figure 2. The seaward boundary of the surf zone was determined by the wave dimensions at $11^{h}\ 00^{m}$ on May 14 1948; period, eight seconds; deep water height, 4.5 feet; breaker height, six feet; depth of breaking, 7.5 feet. If the fluctuations of the tsunami record had been the result of a non-linearity in response of the instrument, the time lag would have been 42 + 30, or 72 sec, approximately half the measured time lag.

In view of the 1000 ft distance separating the swell and tsunami recorders and of other uncertainties, the agreement between the integrated swell record and the tsunami record (see Fig. 4) and between the computed and observed time lag are as good as one might expect. The two- to three-minute oscillations shown by the tsunami recorder appear to be caused by the variability of water transport into the surf zone, and are therefore termed "surf beat." Fluctuations in the speed of longshore currents and rip currents [PUTMAN, MUNK, and TRAYLOR, 1949; SHEPARD and INMAN, in press] are due to the same condition. The variability of the breaking waves results from the variability in the height and period of the waves offshore, and this variability in turn depends essentially on the ratio of storm size to storm distance, and is relatively small for compact storms at large distances.

The shore line acts therefore as a radiating line source which returns approximately one per cent of the incoming wave energy in the form of long-period waves. This is characteristic of the reaction of non-linear systems to high incoming waves. Indeed the surf zone may be considered an extreme case of non-linearity.

The amplitudes of orbital velocity and pressure fluctuation and the double amplitude of horizontal displacements at the sea bottom have been computed for the conditions shown in Figures 2 and 4, assuming the surf beat to travel seaward and being modified according to the usual theory [LAMB, 1932, and U. S. HYDROGRAPHIC OFFICE, 1944]. Results are summarized in Table 2. For depths exceeding 200 ft the greater length of the surf beat more than compensates for its smaller height; at a depth of 500 ft, a typical depth for the outer edge of the continental shelf, the surf beat is associated with 200 times the orbital velocity, and 70 times the pressure fluctuation of that of the incoming waves. At mid-depth in water of 1000-ft depth the vertical accelerations associated with the surf beat and the waves are both approximately $3 \times 10^{-6}g$. The surf beat may be the cause of short-period internal waves, and of surges in harbors.

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